Život v kambriu

The horizontal burrow trace fossil, *Trichophycus* (formerly *Phycodes*) *pedum* defines the lower boundary of the Cambrian in the reference section at Fortune Head, southeastern Newfoundland. It has been suggested that newly evolved, burrowing organisms like this may have closed the taphonomic door on the peculiar 'Ediacaran preservation'. [Image courtesy of Dr. Gerd Geyer, Institut für Paläontologie, Bayerische Julius-Maximilians-Universität, Würzburg, Germany.]

The Cambrian Period is the first period of the Paleozoic Era. It was named in 1835 by the geologist Adam Sedqwick, after the region of Cambria in North Wales, where rocks of this age were first found. The name "Cambria" is a version of *Cumbria*, a latinisation the Welsh *Cymry* (= countryman, compatriot against the (invading) Anglo-Saxons).

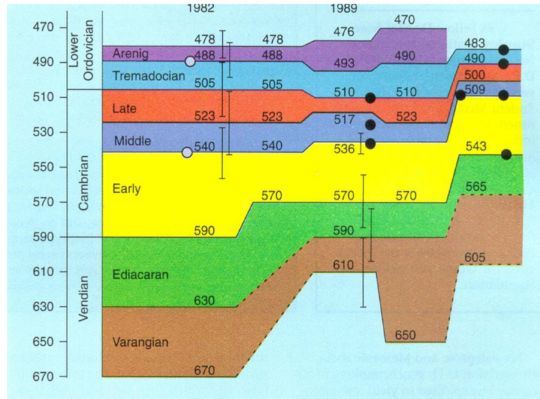
Accordingly, the International Subcommission on Cambrian Stratigraphy (through its Working Group on the Precambrian-Cambrian Boundary) made the official decision in 1991 to draw the base on the Cambrian at the first appearence date (FAD) of *Trichophycus pedum* (formerly known as "*Phycodes pedum*"). in the reference section at Fortune Head. southeastern Newfoundland, which belonged to the Cambrian continent Avalonia

Stratotyp báze kambria

Fortune Head
Newfoundland
Canada

The top of the Cambrian
Definition of the Cambrian-Ordovician boundary was a basic problem dealt with by the Cambrian-Ordovician Boundary Working Group for a long period. Traditional concepts of the Cambrian-Ordovician boundary based on the occurrence of the graptolite ***Rhabdinopora flabelliforme*** (formerly known as *Dictyonema flabelliforme*), which has a limited regional distribution. Strata with *Rhabdinopora flabelliforme* are often difficult to correlate precisely so that different species (and subspecies) of conodonts were favored for definition of the Cambrian-Ordovician boundary. The Cambrian-Ordovician Boundary Working Group finally decided in 1998 by majority that the base of the Ordovician should be placed at the base of the zone with ***Iapetognathus fluctivagus***, which approximates the *Cordylodus lindstromi* Zone, the *Rhabdinopora flabelliforme* Zone and the FAD of the trilobite *Jujuyaspis*. The GSSP for this boundary was chosen at the Green Point section, Newfoundland.

Geochronological framework



Latest Proterozoic and base of the Cambrian
595±15 m.y. mid-Dahai Mb., Meishucun, South China (Rb-Sr whole rock age; Zhang et al., 1984)
575±7.6 m.y. volcanics, Carolina Slate Belt, eastern United States (U-Pb age, Kozuch et al., 198)
550±26 m.y. volcanics, Puncoviscana Foldbelt, northwestern Argentina (K-Ar age, Omarini et al., 1996)
551.4±5.8 m.y. rhyolite flow, Mooring Cove Fm., Fortune Bay, Nfld. (isotope dilution U-Pb age; Tucker and McKerrow, 1995)
543.6±0.24 m.y. volcanic breccias, Lessyusa Fm., Nemakit-Dal'dyn Stage, Khorbusuonka, Olenek uplift, Siberia (U-Pb zircon age; Bowring et al., 1993)
535±7 m.y. granitoids, Puncoviscana Foldbelt, northwestern Argentina (U-Pb age, Bachmann et al., 1987)
534.6±0.4 fluvial conglomerates, between Nemakit-Dal'dyn and Tommotian stages, Kharaulakh Mountains, Siberia (U-Pb zircon age; Bowring et al., 1993)
525±7 m.y., max. 539±34 m.y. K-bentonite, Zhongyicun Mb., Dengying Fm., Meishucun, South China (SHRIMP zircon ages; Compston et al., 1992)

Původ biomineralizovaných schránek

Hlavní funkce:

1. **Podpora svalstva**, etc.
2. **Ochrana před vlivy prostředí a predátory**
3. **Pomoc při pohybu**

Skeleton served as an adaptive breakthrough allowing preferential survival and niche exploitation. Adaptive radiation occurred; rapid diversification of forms.

Possible reasons for the advent of skeletonization:

Increasing oxygen levels (Toewe, 1970)

Synthesis of collagen, a fibrous connective tissue in shells, cuticles, carapaces, etc. directly or indirectly requires collagen.

Oxygen priorities

Low oxygen levels: respiration & tissue synthesis

High oxygen levels: oxygen can be used for lower priority things - skeletons, shells, etc.

Oxygen reached critical threshold at this time, eliminating the need for priorities.

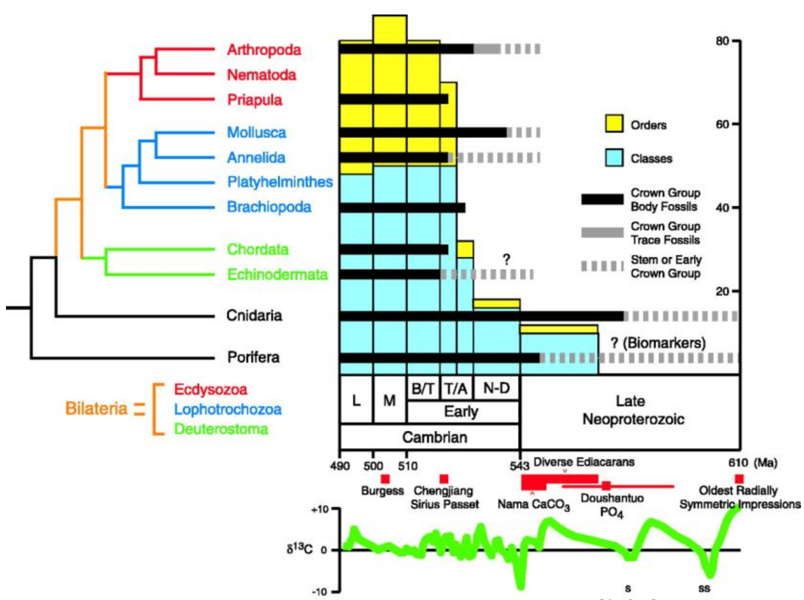
Evidence: modern low O_2 environments have only small, soft-bodied forms.

Kambričtí bezobratlí

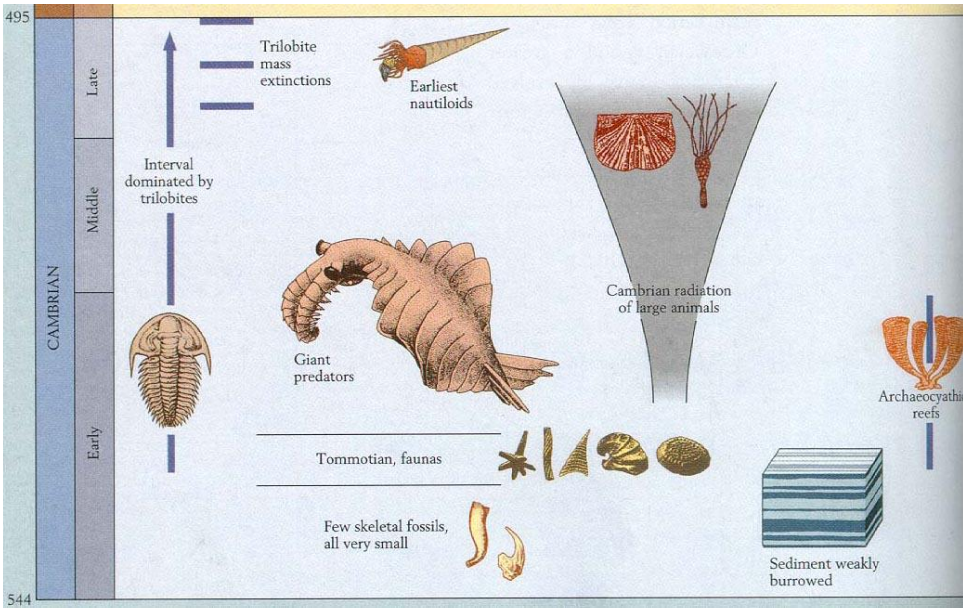
- Kambrium
  - Většina moderních kmenů živočichů
  - Většina moderních tříd se objevuje až v ordoviku
  - Možné vymírání na konci kambria (Signor, 1992)?
    - regrese
    - až 80% druhů ???

Terminal Cambrian Extinctions:
•Mass extinction of trilobites, primitive echinoderms
•Glaciation and anoxia both implicated
•Actually was most likely several pulses of mass extinctions

Evoluční vztahy hlavních skupin bezobratlých na hranici proterozoikum / kambrium



Hlavní události ve vývoji života v kambriu



Tomotská fauna

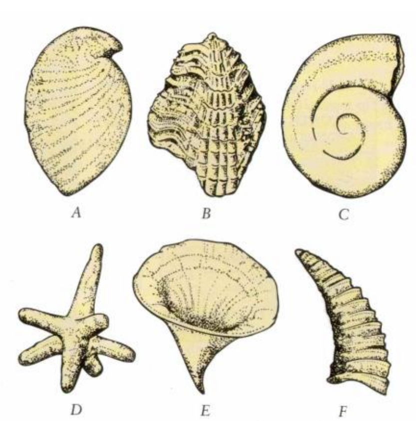


FIGURE 10–13 Late Precambrian and Early Cambrian shell-bearing fossils from Siberia. (A) *Anabarella*, ×20, a gastropod; (B) *Camenella*, ×18, affinity uncertain; (C) *Aldanella*, ×20, a gastropod; (D) sponge spicule, ×30; (E) *Fomitchella*, ×45, affinity uncertain; and (F) *Lapworthella*, ×20. *(After Matthews, S. J. and Missarzhevsky, V. V. J. 1975. Geol. Soc. London 131:289–304.)*

The typical *small shelly fossils* (SSFs, or early shelly fossils, ESFs) are tiny (generally 1 to 5 mm) tubes, spines, cones and plates that are not clearly allied with modern groups. Many of these organisms were recognized either as of unknown affinity or as representatives or groups that became extinct before the end of the Cambrian The most "primitive" stage is marked by characteristic elements, such as anabaritids, tommotiids, and hyolithellids, known as the "Tommotian fauna."

Anabarella (Gastropoda)
Aldanella (Gastropoda)
Spikuly hub (Porifera)

Camenella (???)

CAMBRIAN FOSSILS

1. TRILOBITES
2. ARCHAEOCYATHIDS
3. INARTICULATE BRACHIOPODS
4. HELICOPLACOIDS
5. MONOPLACOPHORANS

In fact, every Phylum known today "evolved" (or is present) in the Cambrian except for the Bryozoa, which appeared in the earliest Ordovician! What are the evolutionary implications of such a record?

Měkkýši

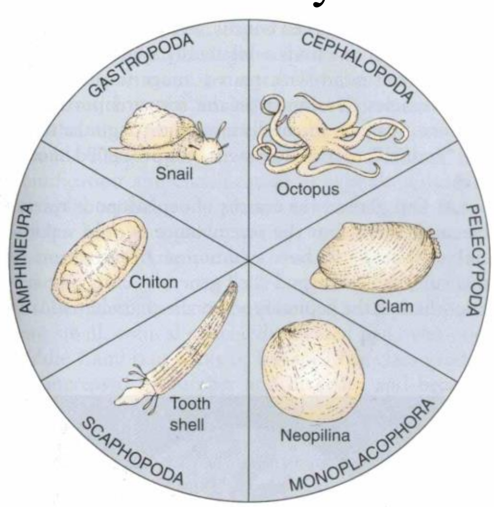
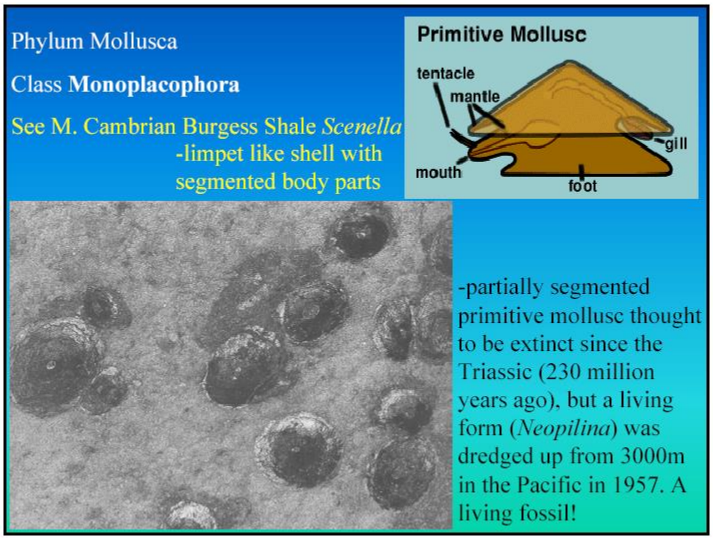


FIGURE 10–40 Some common members of the phylum Mollusca. *(From Levin, H. L. 1975. Life Through Time. Dubuque, IA: William C. Brown Co.)*

Scenella (monoplacophora, přílipky)



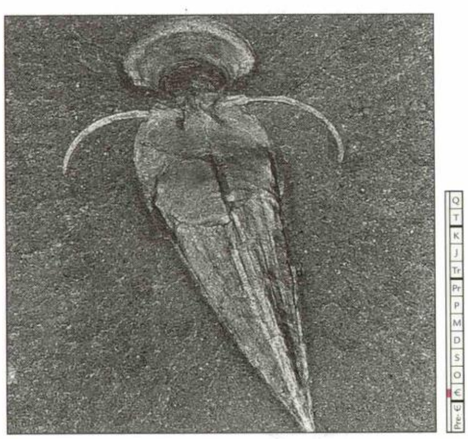


FIGURE 10–16 *Haplophrentis.* This photograph illustrates the nature of preservation of Burgess Shale fossils. *Haplophrentis* had a tapering shell surmounted by a lid or operculum, which could be closed for protection. The lateral blades on either side may have served as props. The length of the shell is 2 cm. *(Courtesy of the U. S. National Museum of Natural History, Smithsonian Institution; photograph by Chip Clark.)*

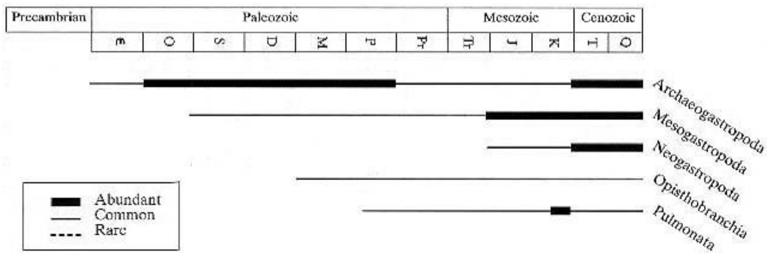
Hyolithes versaillensis

Haplophrentis
Hyolithes

Hyoliti

Order Archaeogastropoda (Lower Cambrian to Recent)

•Possess two nephridia and two auricles
•Radula with large number of unspecialized teeth
•Gills are bipectinate (gill filaments develop on both sides of a central axis)
•Herbivorous
•Shells are planispiral, helical, or cup-shaped
•Order includes the limpet (seen to the right) and the abalone



Gastropodi

Archeocyáti

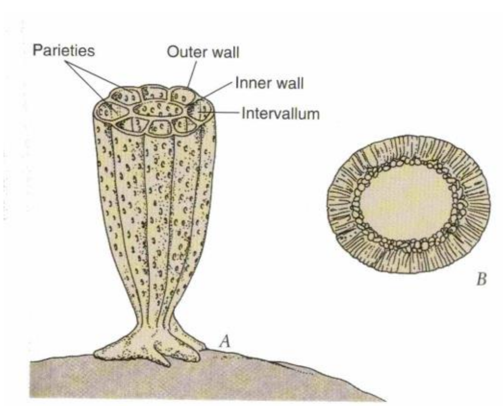
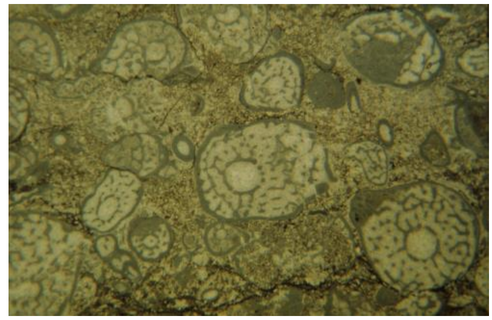


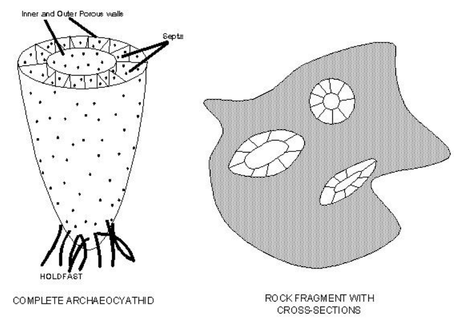
FIGURE 10–25 **The archaeocyathan skeleton.** (A) Longitudinally fluted cup of an archaeocyathan, about 6 cm in height. (B) Transverse section of a nonfluted archaeocyathan having closely spaced parieties and a vesicular inner wall. (Maximum diameter is 4 cm.)

Archeocyathus
Okulitchicyathus

•Reef builders: archaeocyathid sponges (in Early Cambrian only: almost no Middle or Late Cambrian reefs)

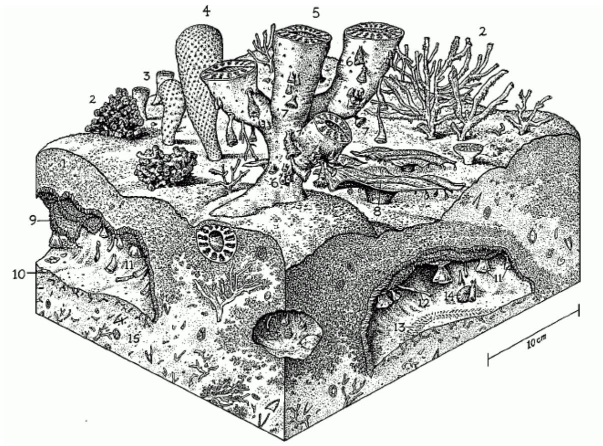
Thin section of archaeocyath "bioherm" showing cross-sections
of archaeocyaths and intergrowing calcimicrobes.
Lower Cambrian Lemdad Formation,
Lemdad syncline, High Atlas, Morocco





Archaeocyaths are an extinct group of sponges that had a very brief (geologically speaking) and spectacular history. The first archaeocyaths appear roughly 530 million years ago, during the Lower Cambrian. Archaeocyath species were very important members of Lower Cambrian communities. They diversified into hundreds of species during this time period and some of these species contributed greatly to the creation of the first reefs. Reef ecosystems tend to support a wide variety of organisms both in the present and in the past. Despite their great success in terms of numbers, the archaeocyaths were a short-lived group. They were almost completely non-existent by the middle Cambrian, some 10 to 15 million years after their first appearance.

Reconstruction of an Early Cambrian reef community (from 97). 1. *Renalcis* (calcified cyanobacterium); 2: branching archaeocyath sponges; 3: solitary cup-shaped archaeocyath sponges; 4: chancellorid (?sponge); 5: radiocyath (?sponge); 6: small, solitary archaeocyath sponges; 7: cryptic "coralomorphs"; 8: *Okulitchicyathus* (archaeocyath sponge); 9; early fibrous cement forming within crypts; 10: microburrows (traces of a deposit-feeder) within geopetal sediment; 11: cryptic archaeocyaths and coralomorphs; 12: cryptic cribricyaths (problematic, attached skeletal tubes); 13: trilobite trackway; 14: cement botryoid; 15: sediment with skeletal debris.



Brachiopodi

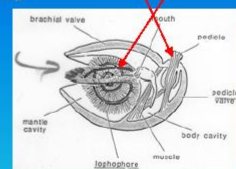
•**Brachiopods**:
•Two-shelled filter feeders
•Dominant groups in Cambrian are “inarticulates”: **linguates** (infaunal forms with calcium phosphate shells) and **craniids** epifaunal forms with calcite shells)
•**Articulate brachiopods** (epifaunal with calcite shells) are present but rare

PHYLUM BRACHIOPODA

Name derived from Latin *Bracchium* (arm) and Greek *pod* (foot).

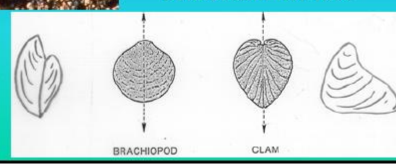
Class Lingulata (Inarticulata); lack tooth and socket and have chitinophosphatic shell

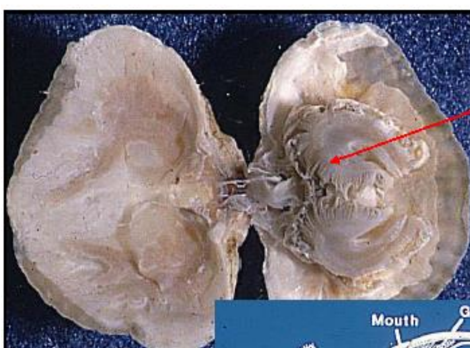
Class Articulata; tooth and socket and calcareous shell, 95% of genera



-but the lophophore support and pedicle are neither arm nor foot

Have two valves like clams (Phylum Mollusca), but very different planes of symmetry (across valve rather than between).





Specialized ciliated feeding structure or lophophore, for these filter feeding metazoans

Brachial (dorsal) and

Pedicle (ventral) valve

Lingulella ampla

svrchní kambrium
Eau Claire Form. Colfax. Wisconsin.
USA.

Bohemiella roemingeri
Barrandien, Česká republika, střední kambrium

PALEOECOLOGY

- Benthic marine, sessile filter-feeders.
- Articulates are normal marine.
- Inarticulates often lived in stressed hypo- or hypersaline settings and burrowed.
- Most require a hard substrate to settle.
- Strophomenids did not have large pedicle openings and lived on soft-substrates.

Most Cambrian communities are dominated by trilobites and other deposit feeders that lived near the sediment-water interface. That would change in the Ordovician. In addition, 90% of fossils in normal Cambrian sites are trilobites and brachiopods, but the Middle Cambrian Burgess Shale says this is not a normal community structure.

Trilobiti

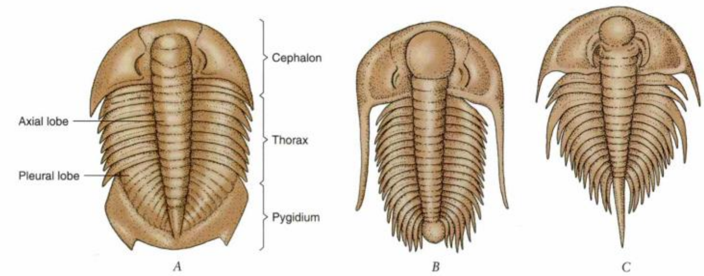


FIGURE 10–49 **Three well-known Cambrian trilobites.** (A) *Dikelocephalus minnesotensis* (Upper Cambrian), (B) *Paradoxides harlani* (Middle Cambrian), and (C) *Olenellus thompsoni* (Lower Cambrian).

•Trilobites:
•Group of arthropod found only in Paleozoic
•EXTREMELY common in Cambrian and Ordovician; still common but lower diversity in rest of Paleozoic
•Benthic epifaunal detritovores (backwards facing mouth).
•Known from many growth stages, thousands of species, trace fossils, etc.
•**The main index fossils of the Cambrian.**

Olenellus fowleri, Lower Cambrian,
Pioche Formation, Lincoln County, Nevada

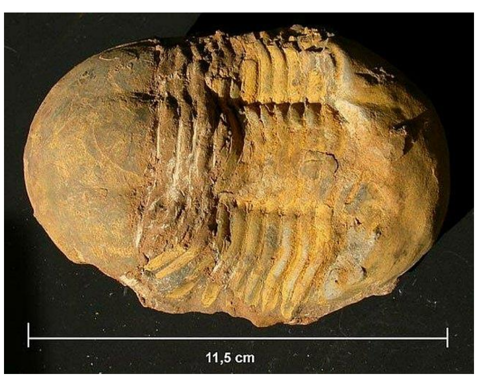
Ptychoparia striata #252
Middle Cambrian, 530 million years old
Jince, Czech Republic

Hydrocephalus minor
Middle Cambrian, 530 million years old
Jince, Czech Republic

Paradoxides gracilis
Middle Cambrian, 530 million years old
Jince, Czech Republic

Ellipsocephalus hoffi

Eccaparadoxides
M. Cambrian
Location: France

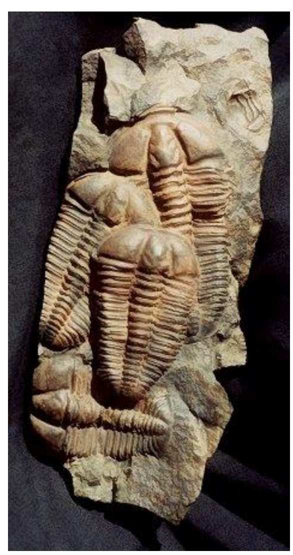


Olenus

Conocoryphe sulzeri #253
Middle Cambrian, 530 million years old
Jince, Czech Republic

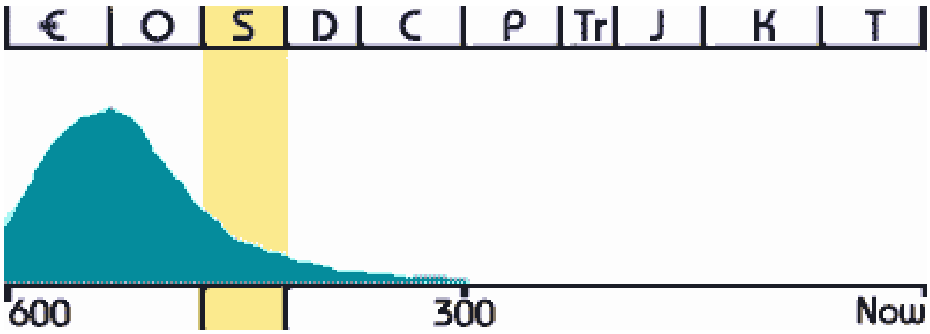
Sao hirsuta, Middle Cambrian, Skryje

Sao hirsuta



Conocoryphe sulzeri

Trilobite diversity



Phylum Echinodermata

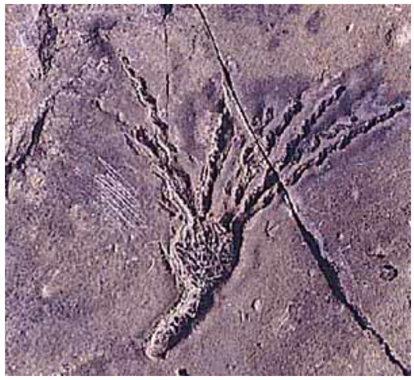
Subphylum **Blastozoa**
..........Class **Eocrinoidea** (Cambrian - Silurian, 30-32 genera)
..........Class Parablastoidea (Ordovician, 3 genera)
..........Class Rhombifera = Cystoidea in part (Ordovician - Devonian, 60 genera)
..........Class Diploporita = Cystoidea in part (Ordovician - Devonian, 42 genera)
..........Class Blastoidea (Silurian - Permian, 95 genera)

Subphylum **Crinozoa**
..........Class **Crinoidea** - sea lilies (Cambrian? Early Ordovician - Recent, 1005 genera)
..........Class Paracrinoidea (Ordovician - Silurian, 13-15 genera)

Subphylum **Echinozoa**
..........Class Echinoidea (Sea Urchins) (Ordovician - Recent, 765 genera)
..........Class Holothuroidea (Sea Cucumbers) (Ordovician - Recent, 200 genera)
..........Class **Edrioasteroidea** (Early Cambrian - Carboniferous, 35 genera)
..........Class Edrioblastoidea (Ordovician, 1 genus)
..........Class **Helicoplacoidea** (Cambrian, 3 genera)
..........Class Cyclocystoidea (Ordovician - Devonian, 8 genera)

Subphylum Asterozoa (= Stelleroidea)
..........Class Asteroidea - starfish - (Early Ordovician - Recent, 430 genera)
..........Class Ophiuroidea - Brittle Stars -(Ordovician - Recent, 325 genera)

Subphylum **Homalozoa**
..........Class **Stylophora** (Cambrian - Devonian, 32 genera)
..........Class **Homoiostelea** (Cambrian - Devonian, 12-13 genera)
..........Class **Homostelea** (Cambrian, 3 genera)
..........Class **Ctenocystoidea** (Cambrian, 2 genera)

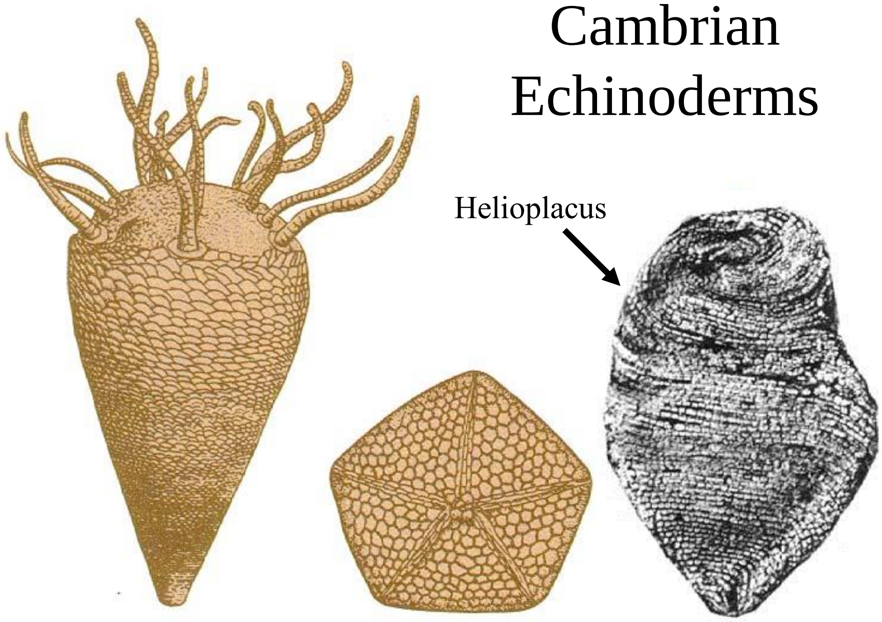


Pralilijice (eocrinoidea)

Eocrinoids are among the earliest groups of echinoderms to appear, ranging from the Early Cambrian to the Silurian. This one, **Gogia**, is from the Middle Cambrian House Range of Utah

Echinoderms:
Deuterostomes with five-fold body symmetry, calcite test, and a specialized water-vascular system
Most Cambrian echinoderms were stalked (and thus sessile), but some were motile

Cambrian Echinoderms



Burgesská fauna

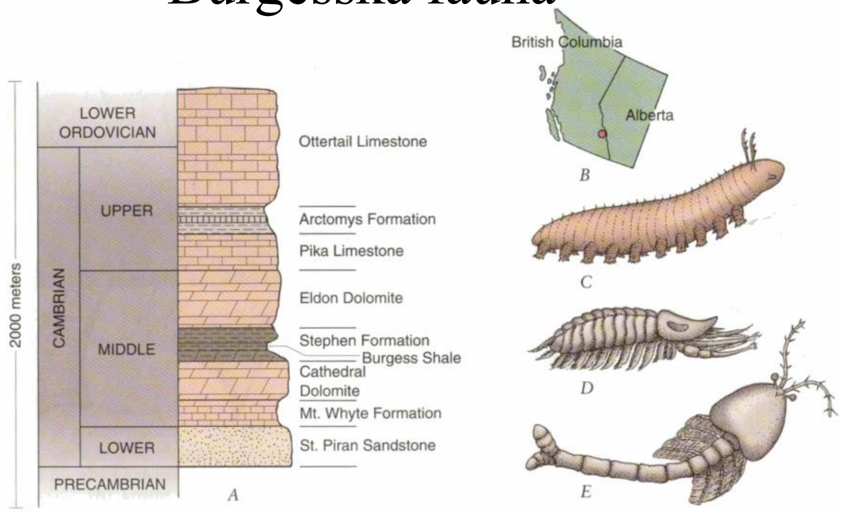
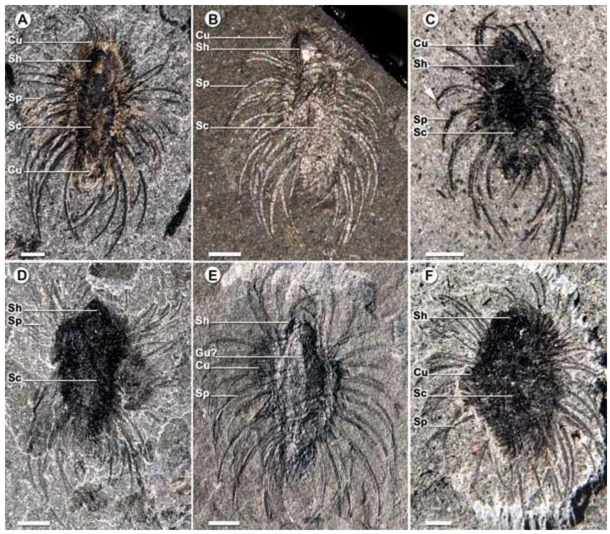


FIGURE 10–15 The Cambrian geologic column (A) at Kicking Horse Pass, British Columbia (B) where Walcott discovered the Burgess Shale Fauna. *Aysheaia* (C) is an invertebrate called an onycophoran or velvet worm. They are of particular interest because they appear to be intermediate in evolution between segmented worms and arthropods. *Leanchoila* (D) and *Waptia* (E) are among the many kinds of arthropods found at this locality.

Burgess Pass


BURGESS SHALE · SCHISTES DE BURGESS
YOHO NATIONAL PARK · PARC NATIONAL YOHO
WORLD HERITAGE SITE · SITE APPARTENANT AU PATRIMOINE MONDIAL
BURGESS SHALE WAS PLACED ON THE WORLD HERITAGE LIST AT THE 1980 MEETING OF THE UNESCO WORLD HERITAGE COMMITTEE AS A SITE OF OUTSTANDING UNIVERSAL VALUE FORMING PART OF THE NATIONAL HERITAGE OF MANKIND.
DATING FROM MIDDLE CAMBRIAN TIME, MORE THAN 500 MILLION YEARS AGO, IT IS ONE OF THE WORLD'S MOST SIGNIFICANT FOSSIL SITES. IT HAS YIELDED MORE THAN 150 SPECIES OF SOME 120 GENERA. THE REMARKABLY PRESERVED SOFT-BODIED MARINE ANIMALS, UNIQUE TO BURGESS SHALE, ARE OF MAJOR IMPORTANCE TO EVOLUTIONARY BIOLOGY.
PATRIMOINE MONDIAL DE L'UNESCO EN 1980 EN RECONNAISSANCE DE SA VALEUR UNIVERSELLE EXCEPTIONNELLE POUR LE PATRIMOINE MONDIAL.
CET EMPLACEMENT, QUI REMONTE À LA PÉRIODE CAMBRIENNE, EST L'UN DES PLUS IMPORTANTS DÉPÔTS FOSSILIFÈRES AU MONDE. ON Y A DÉCOUVERT PLUS DE 150 ESPÈCES ISSUES D'ENVIRON 120 GENRES DIFFÉRENTS. L'EXCELLENT ÉTAT DES FOSSILES D'ANIMAUX MARINS À CORPS MOU QU'ON NE TROUVE QU'ICI EST D'IMPORTANCE CAPITALE POUR LA BIOLOGIE ÉVOLUTIONNAIRE.


YOHO
Fossils of the
Burgess Shale



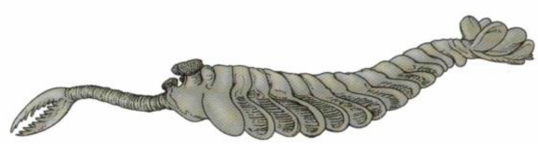


FIGURE 10–20 *Opabinia.* This strange Burgess Shale animal had a frontal "nozzle" with a jawlike structure at its end used for gathering food. There were five eyes on its head. Each side was covered with overlapping lobes bearing narrow stripes interpreted as gills. This specimen was 7 cm long. *(Adapted from Whittington, H. B. 1975.* Philosophical Transactions of the Royal Society of London, vol. B.)

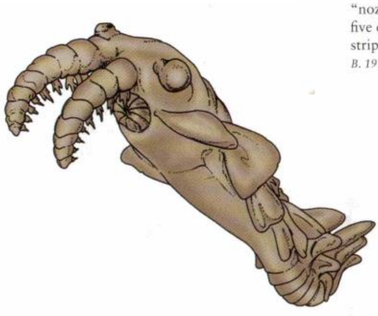


FIGURE 10–19 *Anomalocaris.* This giant predator (often 60 cm in length) captured its prey with its huge frontal appendages and passed the victims back to the circular mouth with its outer and inner circles of teeth. The side flaps were used in swimming, like underwater wings.

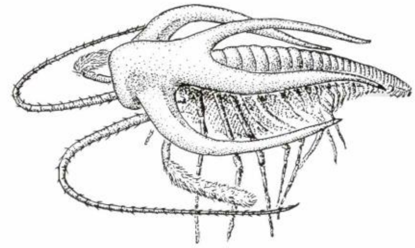


FIGURE 10–21 *Marrella,* **the most common arthropod in the Burgess Shale fauna.** The animal was about 2 cm in length.

Marella

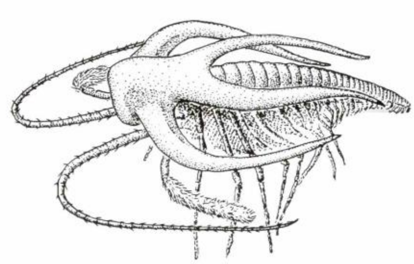
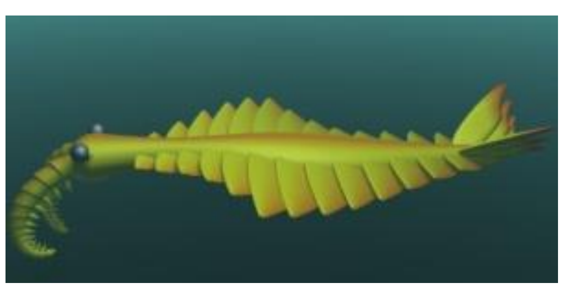


FIGURE 10–21 *Marrella*, **the most common arthropod in the Burgess Shale fauna.** The animal was about 2 cm in length.



Anomalocaris canadensis

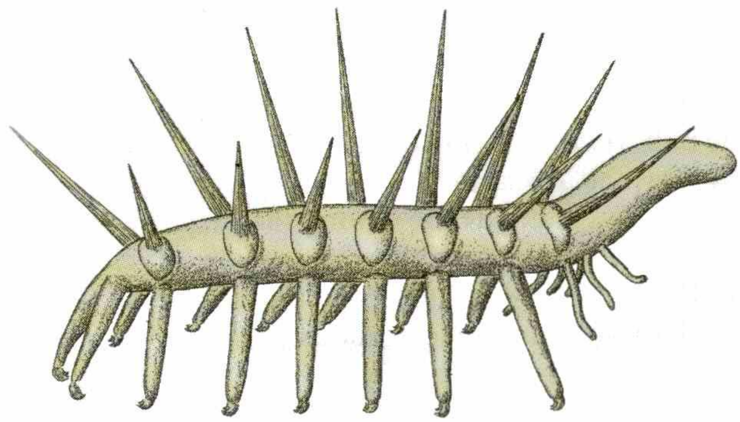
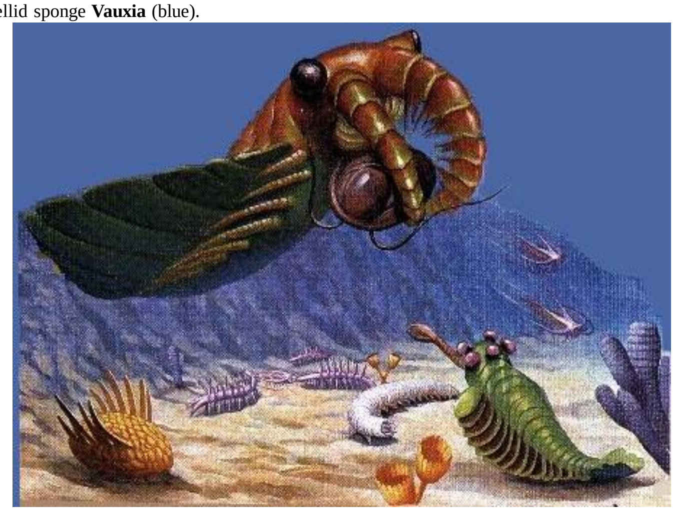


FIGURE 10–22 The early Cambrian Burgess Shale fossil *Hallucigenia.*

mid Cambrian scene, a **reconstruction** of the famous **Burgess Shale lagerstätten** of what is now British Columbia.

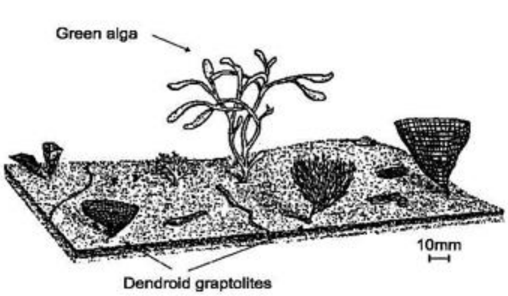
In the foreground a swimming **Laggania cambria** has captured a hapless trilobite. On the sea floor from left to centre respectively are a solitary specimen of the **proto-annelid Wiwaxia** and three specimens of the lobopod **Hallucigenia**. Note in both animals the defensive array of spines. Further to the right is the lobopodian **Aysheaia** with its anterior prongs around the mouth, as well as the protoarthropod **Opabina**, a close relative of Laggania Descending to the sea floor are two individuals of the basal arachnomorph **Marrella**. Also visible in this scene are sessile epifauna in the form of the deuterostome lophophorate **Dinomischus** (yellow) and the Hexactinellid sponge **Vauxia** (blue).

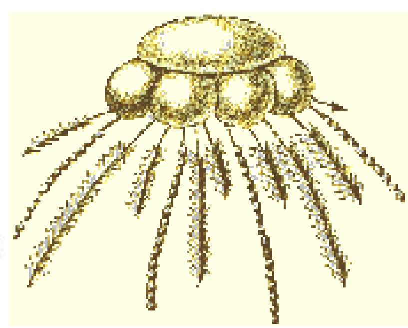


https://www.youtube.com/watch?v=3aLd8NN0YtY

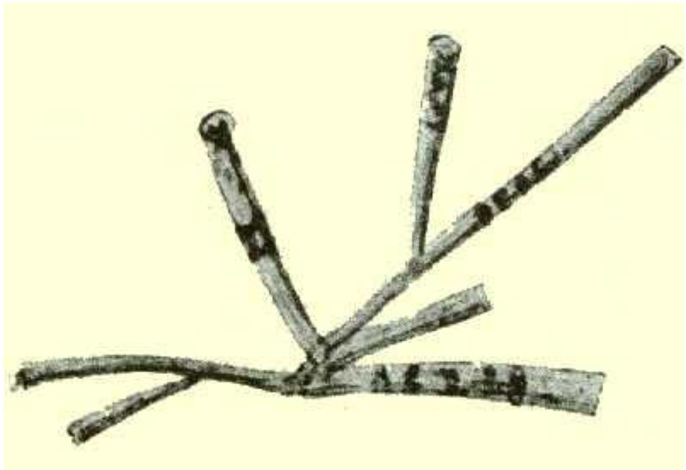
Graptolites

Graptolites range from the middle Cambrian to the Carboniferous. Dendroidea are found across this entire span while Graptoloida are found from the Ordovician until the earlyDevonian. Graptolites are most commonly found in deep water, dysoxic facies (black shales), but do extend into shallow facies. Because they did not biomineralize an easily preservable skeleton they are nearly always carbonized. The process of carbonization combined with the highly compressible nature of shales made most graptolite fossils extremely flat and therefore difficult to study.





Haplograptus wisconsinensis
Cambrian, Wisconsin, U.S.A. Holotype.



Strunatci

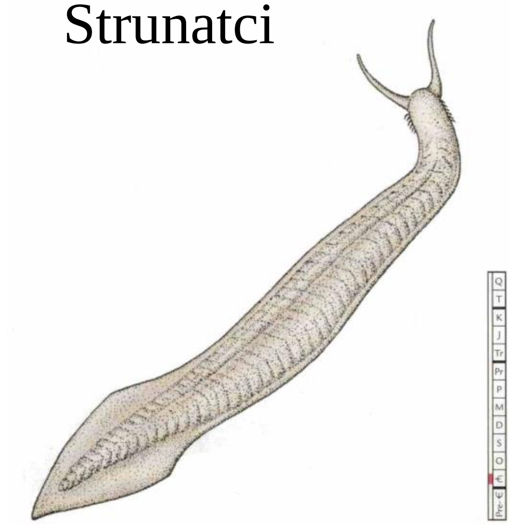
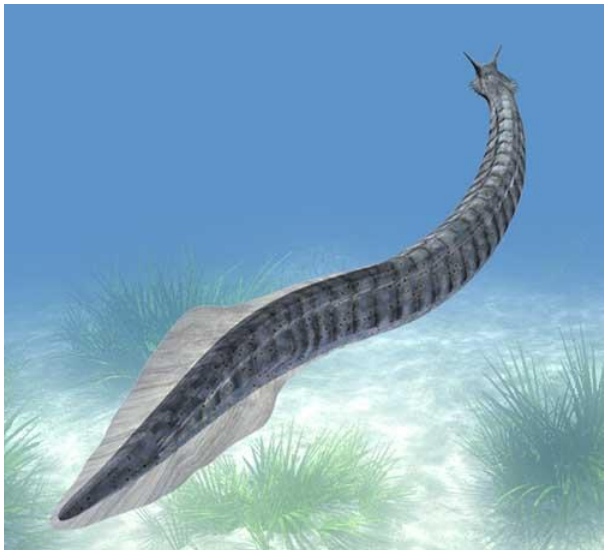
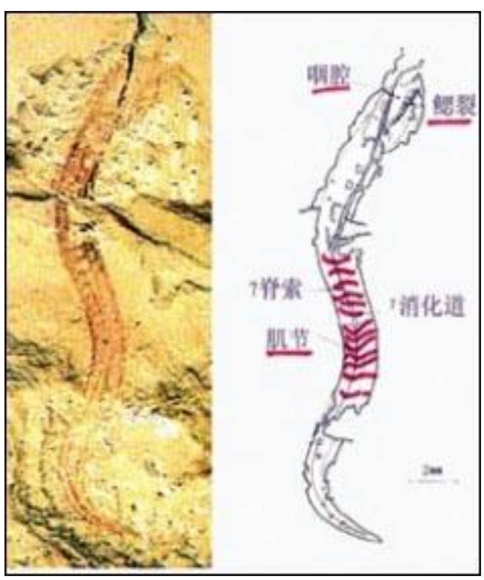


FIGURE 10–18 **Reconstruction of *Pikaia*, the earliest known member of our own phylum, the Chordata.** Note the rod along the animal's back that appears to be a notochord (Length is about 4 cm.) Name another chordate feature seen in *Pikaia* fossils.

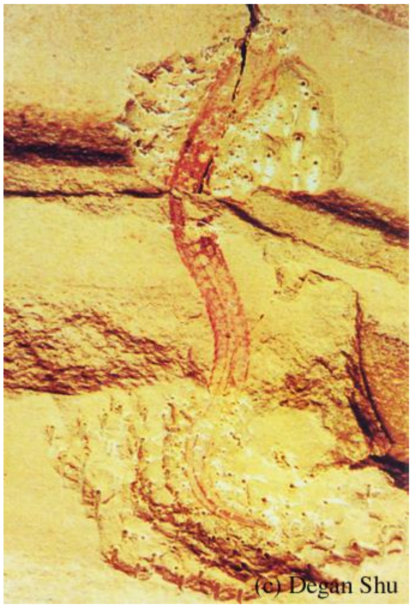


Pikaia



Early Cambrian (about 530 million years ago)

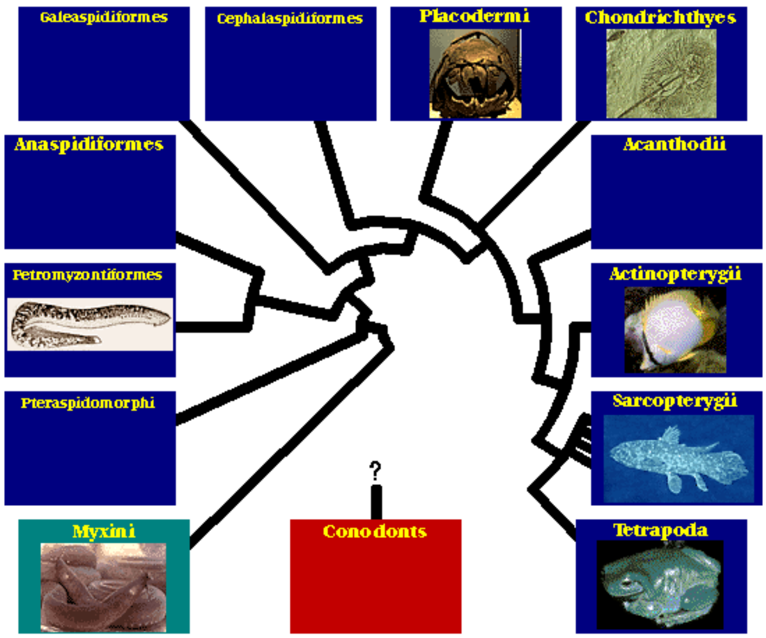
This is oldest known example of a **cephalochordate**. The form of ***Cathaymyrus*** resembles that of *Pikaia* from the Middle Cambrian Burgess Shale of Canada, but this animal is about 10 million years older. Some palaeontologists have suggested that the vertebrates, which include humans, evolved from cephalochordates like *Cathaymyrus*



Cathaymyrus diadexus
Early Cambrian (about 530 million years ago)

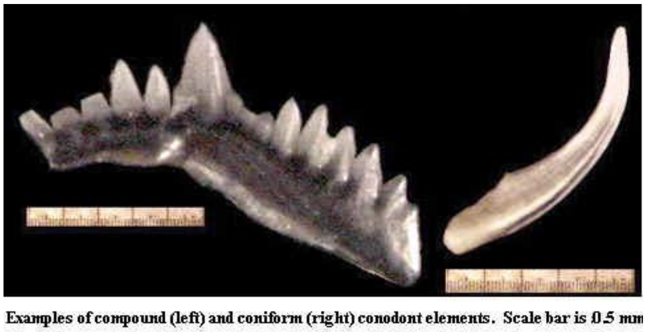
AGNATHA (jawless "fish"):
•Cambrian vertebrates known from bony plates and impressions of lamprey-like forms from Chengjiang.
Most Cambrian organisms are only known from their hard parts, but the Early Cambrian **Chengjiang** site in China and the Middle Cambrian **Burgess Shale** in British Columbia preserve soft-tissue impressions.
AGNATHA (***Ostracoderms***) - Upper Cambrian of Wyoming

The first vertebrate known is the Upper Cambrian fossil Anaspis, over 500 million years old



CONODONTS

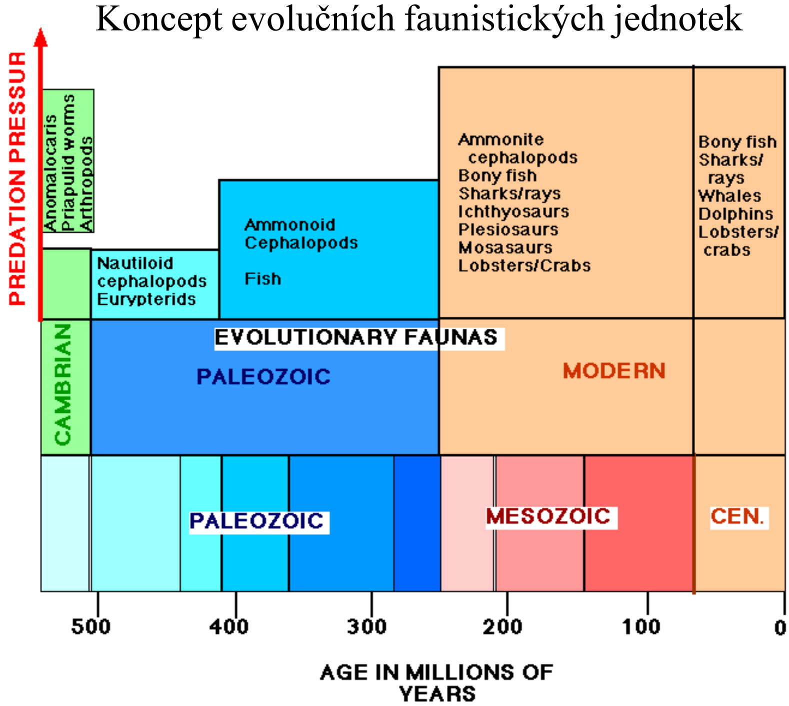
- conodonts are small tooth shaped structures
  - have been found in fossil record for many years
  - important biostratigraphically
  - made of phosphate (like most vertebrate bones)
  - conodont teeth with soft “worm-like” parts found in Scotland (in a museum drawer) (Clarkson, 1983)
  - Ordovician conodont over 1 foot long (1995)
  - probably a predator in Chordata



Conodonts (appear in Late Cambrian):
A group of chordates, very likely craniates, and possibly even vertebrates
Known almost exclusively from their hard (calcium phosphate) tooth-like elements
Soft tissue preservation allows us to see that they had flattened elongate "eel-like" bodies
Were probably fast swimming micropredators
Survived until end of the Triassic.

Vývoj života ordovik - devon

Koncept evolučních faunistických jednotek



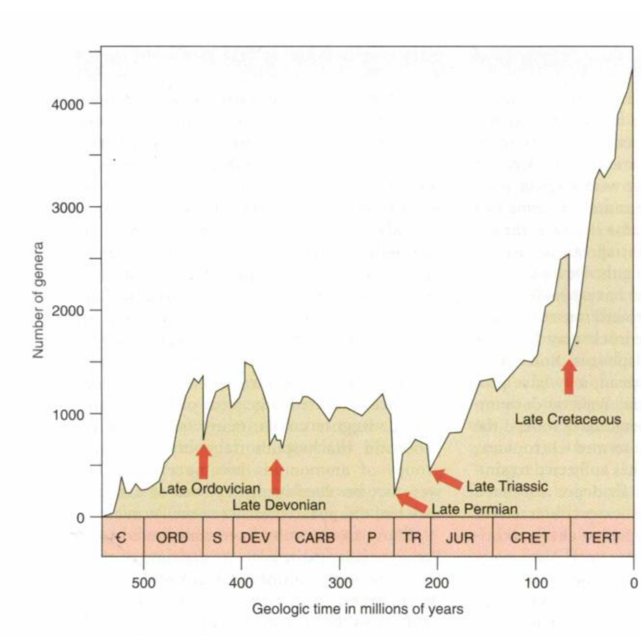


FIGURE 10–84 Diversity of marine animals compiled from a database recording first and last occurrences of more than 34,000 genera. The graph depicts five major episodes of mass extinction (global extinctions over a short span of geologic time). *(Adapted from Sepkoski, J. J., Jr. 1994. Geotimes 39(3):15–17.)*

The Early Ordovician was a time of **adaptive radiation** of many faunal groups, following the mass extinction of trilobites and nautiloids at end of Cambrian.
Increase in diversity from 150 families -> 400 families

•The **Paleozoic fauna** (or **Brachiopod fauna**): articulate brachiopods, stony and lacy bryozoans, stromatoporoids, cephalopods, crinoids and blastoids, starfish, graptolites

Important Groups of Paleozoic Invertebrates

- Porifera – Sponges
- Cnidaria – Corals (Rugosa and Tabulata)
- Bryozoa – Moss animals
- Brachiopoda – Lamp shells (Articulata and Inarticulata)
- Arthropoda – Trilobites, Crustaceans, Insects
- Mollusca – Snails, Bivalves, Cephalopods
- Echinoderms – Crinoids and Blastoids

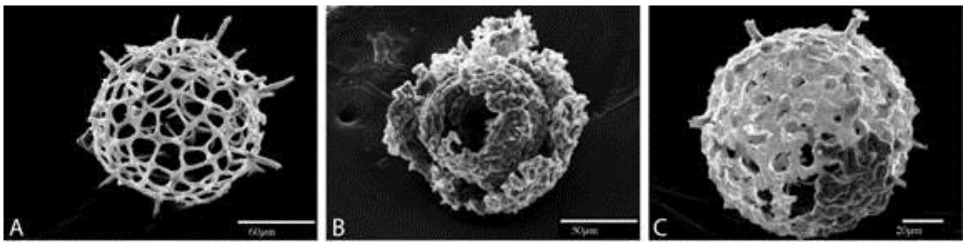
Foraminifera

Protozoa

Nanicella, sv. devon

Radiolaria

- In Paleozoic only Nasselaria
- Rock-forming role in the Devonian – radiolarites
- E.g. Ponikev Formation.



Arthropoda

Subphyla Trilobita
Trilobites **(extinct)**
UCMP - Trilobita

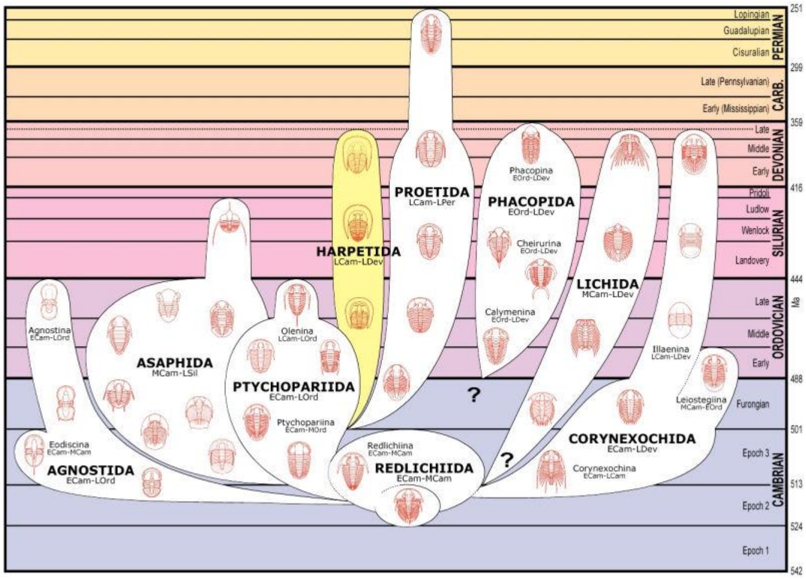
Subphyla Crustacea
Shrimp, lobsters, crabs, barnacles, **cladocerans, ostracoids,** crayfish, **water fleas, and copepods**
Characteristics
Branched antennae
Mandibles (chewing mouth parts)
Encarta Online - Crustacea

Subphyla Chelicerata
Spiders, scorpions, ticks, mites, **sea spiders, and** horseshoe crabs
Characteristics
Lack antennae
Chelicerae (pincerlike mouth parts)
UCMP - Chelicerata
Encarta Online - Chelicerata

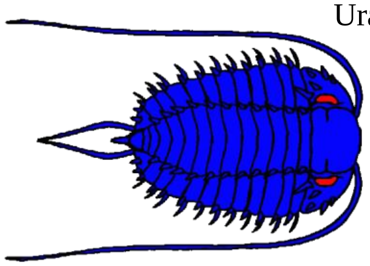
Subphyla Uniramia
Insects, centipedes, **and** millipedes
Characteristics
Antennae
Mandibles
Unbranched appendages

Trilobites

- Still abundant and stratigraphically important.
- Second and last prime in early Devonian
- since middle Devonian on retreat

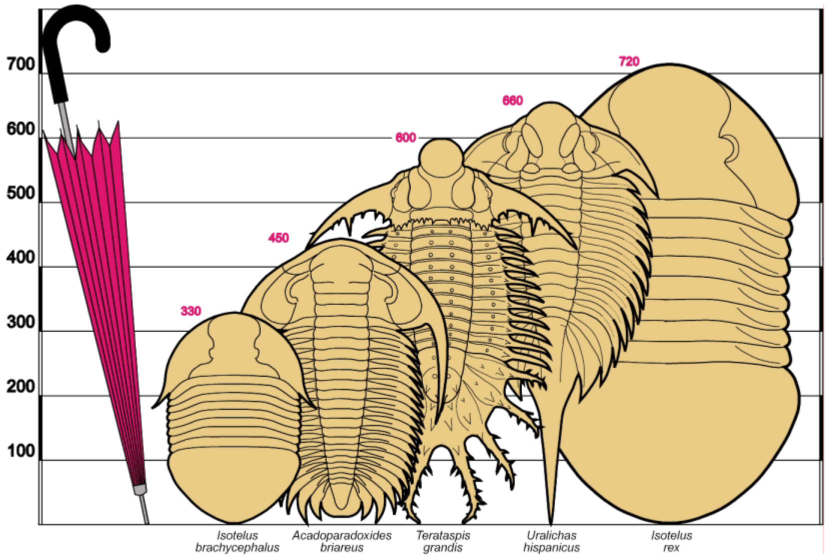


Uralichas

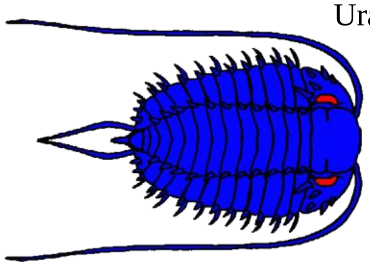


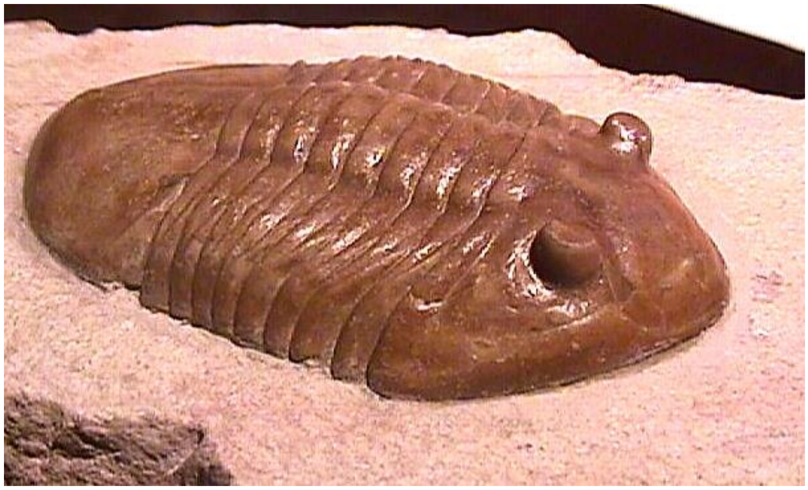
Ordovician

Selenopeltis


700
600
500
400
300
200
100
720
660
600
450
330
Isotelus brachycephalus
Acadoparadoxides briareus
Terataspis grandis
Uralichas hispanicus
Isotelus rex

Uralichas



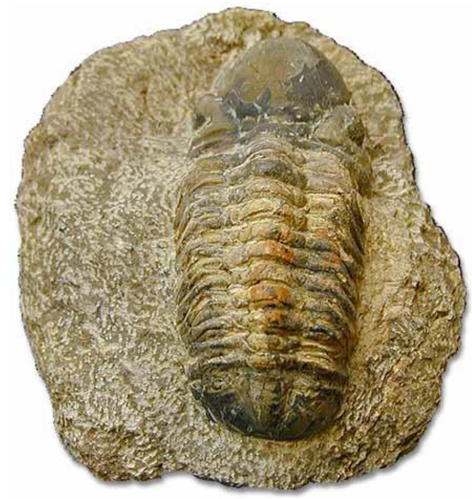


Asaphus

Aulacopleura konincki,
Silur,

Phacops

DEVONIAN



Reedops

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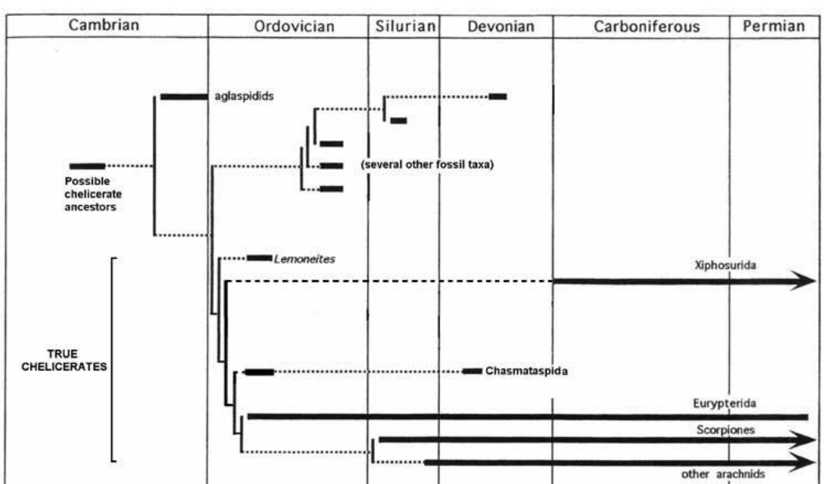
Odontochile

Chelicerata
- Merostromata
  - Eurypterida

Eurypterida, evoluce



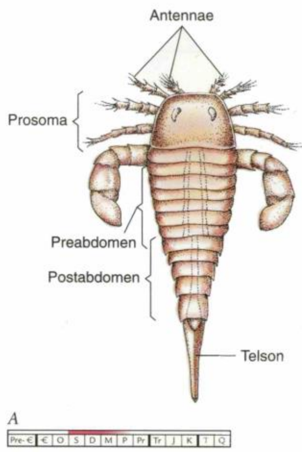
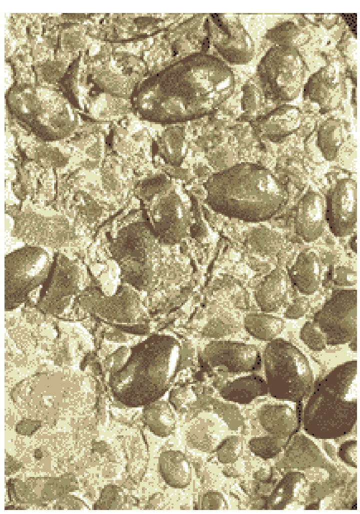


FIGURE 8–31 **Two genera of eurypterids.** *Eurypterus* (A) is noted for its broad, flipperlike paddles and blunt frontal margin. *Pterygotus* (B) is distinguished by a pair of formidable-looking frontal pincers. The animal swimming in the center background is a primitive jawless fish. *(Drawing and model of* Eurypterus, × *1/3. Reconstruction of* Pterygotus *courtesy of the National Natural History Museum, Smithsonian Institution.)*

Ostracodes

Since Ordovician diversification of ostracodes

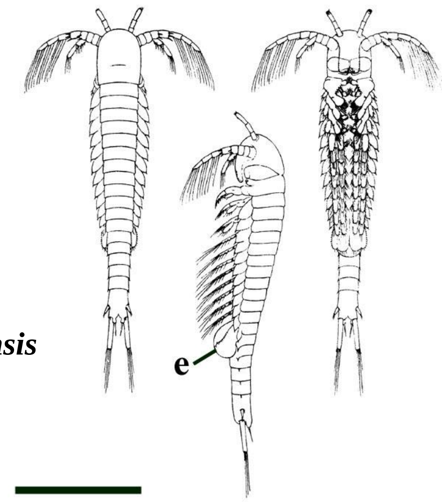


- ***Eoleperditia fabulites* Conrad**
- Middle Ordovician, Rutherford Co., Tennessee
- Shells are bivalved, small (1 to 10 mm) and oval
- Recrystallization

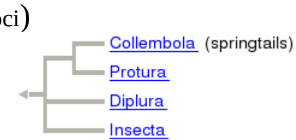
Branchiopoda (lupenonožci) je skupina primárně sladkovodních korýšů - devon

First Decapoda in the late Devonian

Lepidocaris rhyniensis



Insects – Apterygota (Colembola Chvostoskoci)



Insect evolution: Six legs good
Primitive **insect-like creatures** called springtails were among the earliest known animals to colonize the land, early in the Devonian period almost **400 million years ago**.

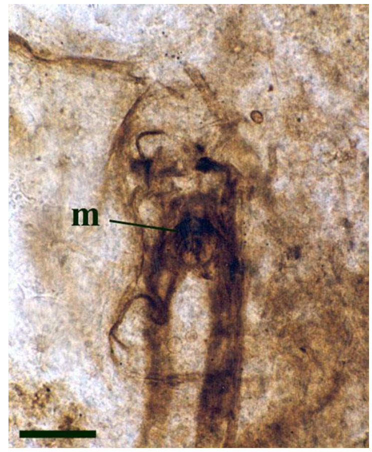
New light shed on the oldest insect
MICHAEL S. ENGEL & DAVID A. GRIMALDI
Nature **427,** 627–630 (2004); doi:10.1038/nature02291

In contrast, fossils of the earliest known **true insects** are known from later on in the Devonian period. However, reinterpretation of a fragmentary insect fossil from the important **early Devonian Rhynie cherts** of Scotland shows that the enigmatic

Rhyniognatha hirsti

was not only a **true insect**, **but relatively derived** — that is it had been around long enough to have accumulated some uniquely insect-like features. Although only the mandibles are preserved, it is possible that they once belonged to a winged insect. In any case, the fossil shows that the origin of insects was much earlier than previously thought.

The discovery suggests that insects almost certainly evolved in the **Silurian Period**, some 438-408 million years ago.



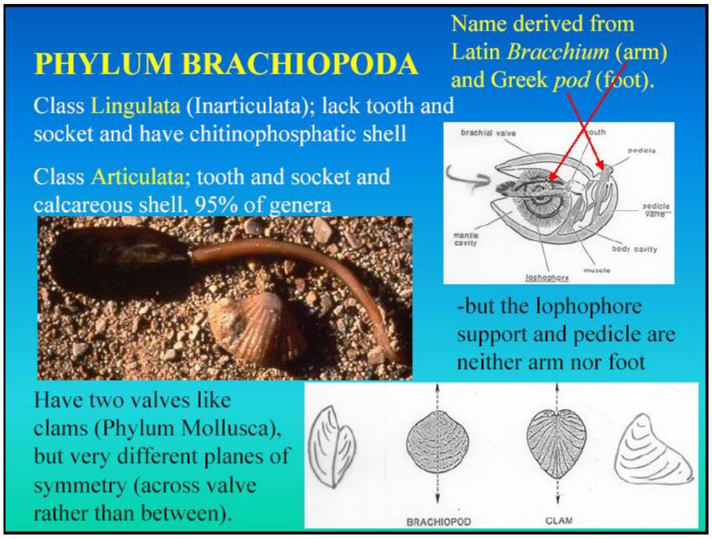
Arachnids

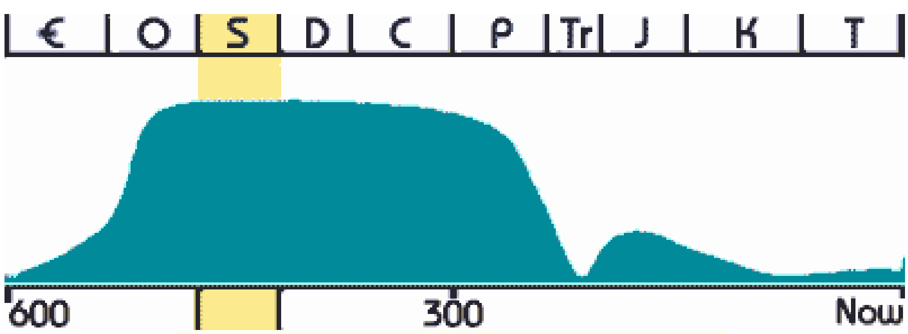
Late Devonian

Gigantocharinus

Brachiopodi

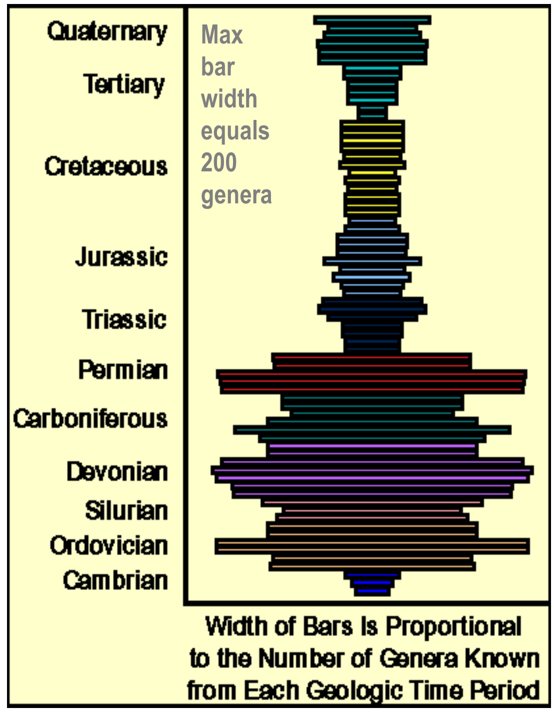
Diverzifikace artikulátních brachiopodů

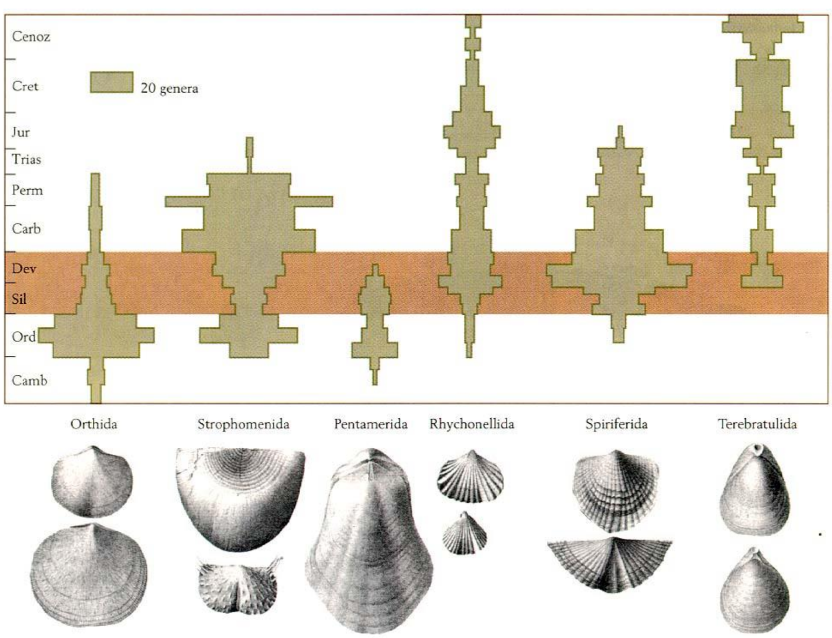




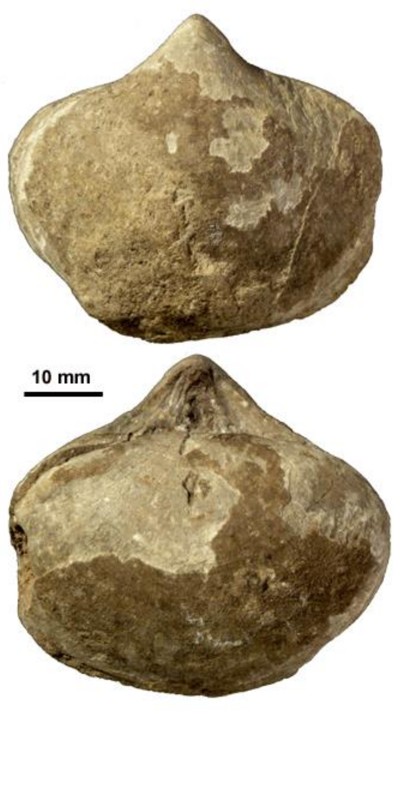
Adaptivní radiace brachiopodů v ordoviku

Brachiopod abundance through geologic time





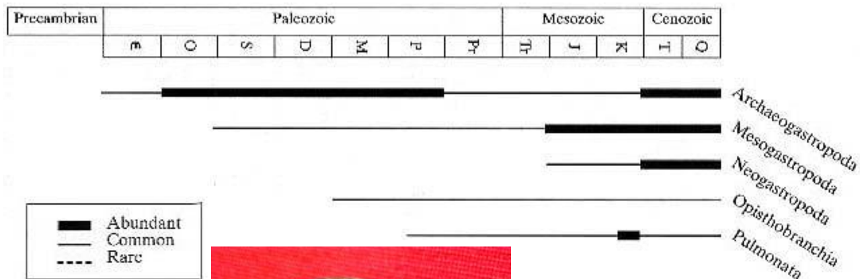
Strophomena



Stringocephalus

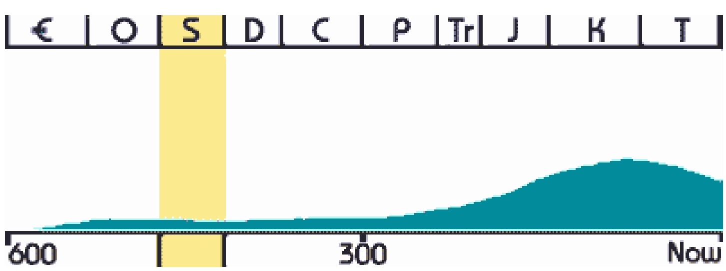
Gastropodi

Gastropods - they appear in the Cambrian but are not abundant until the Late Paleozoic.

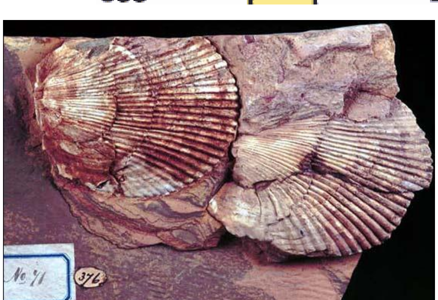


Platyceras

Mlži



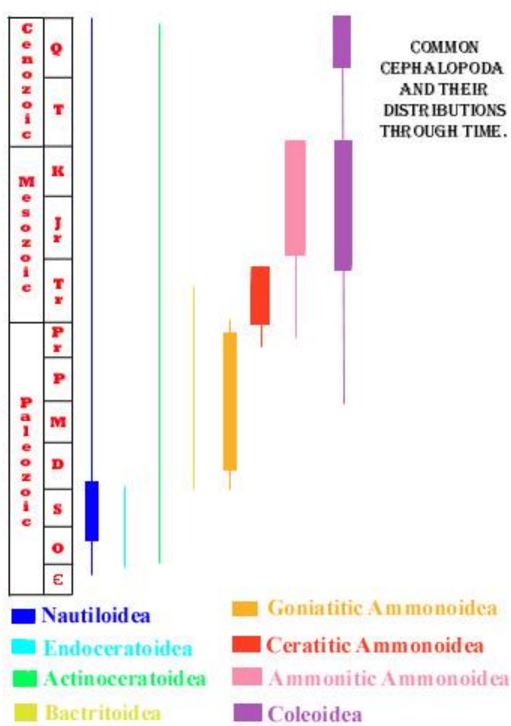
Cardiola



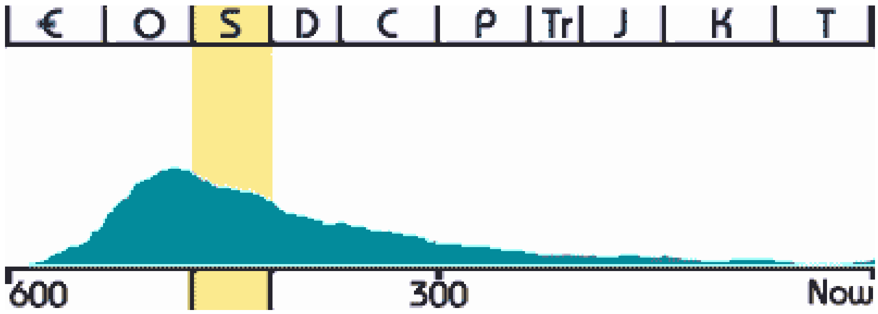
Panenka

Tentakuliti

Hlavonožci

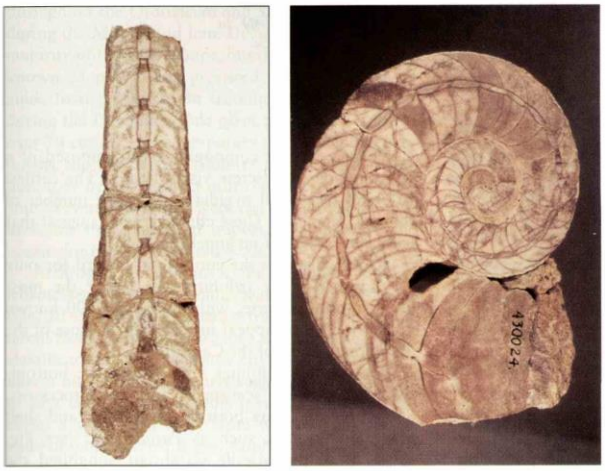


Nautiloidi



Lituites littuus, an odd nautiloid fossil from the Ordovician of China.

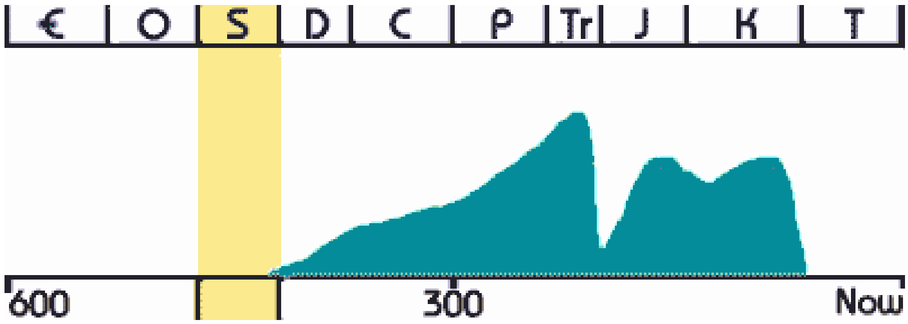
Obří nautiloidi

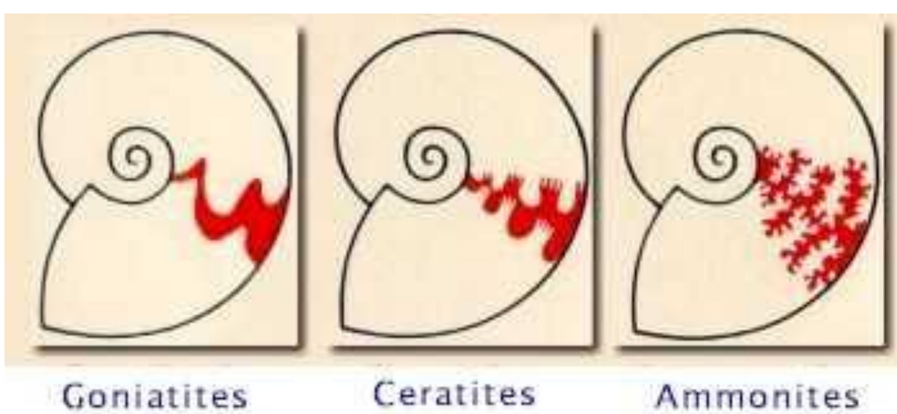


A B

FIGURE 10–46 Variation in conch shape among early Paleozoic nautiloid cephalopods. Both of these specimens are from the Silurian of Bohemia. (A) A sawed and polished section of the straight conch of *Orthoceras potens* showing septa and siphuncle. (B) Sawed and polished section of *Barrandeoceras*, exhibiting a coiled form. Specimen A is 22.5 cm in length; B has a diameter of 18 cm.

Ammonoidi





Clymenia

The goniatite *Goldringia* is at center. Behind, the straight-shelled cephalopod *Michelinoceras* is can be seen. At front left, the trilobite *Phacops* is moving near a cluster of *Paraspirifer* brachiopods

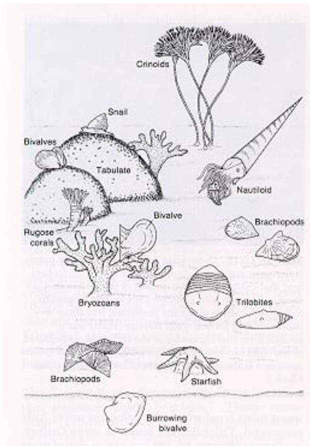
Sépie

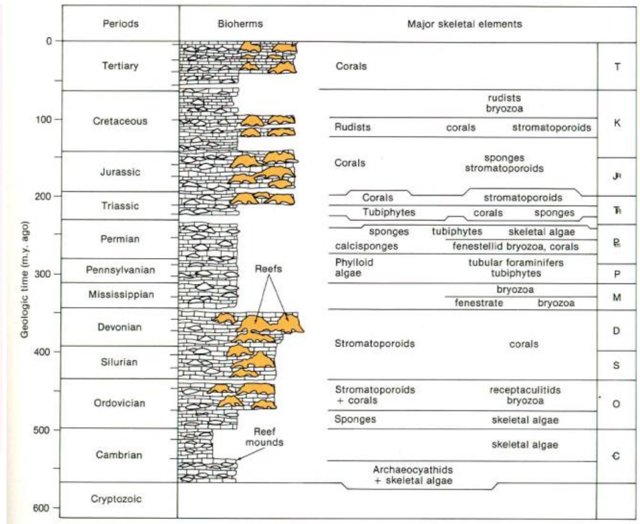
Devonian Eoteuthis

Alloteuthis

Ordovician reefs

First True Reefs





Bryozoa **Moss Animals, Sea Mats,**

Stenolaemata - Cyclostomata Fenestrata Cryptostomata Cystoporata Trepostomata

Gymnolaemata - Ctenostomata Cheilostomata

Phylactolaemata

Bryozoa

Bryozoan Classification - **Class Stenolaemata**

Marine bryozoans with tubular zooids with calcified walls. Lophophore is protruded by action of annular muscles. Includes five sub-groups:

- **Trepostomata:** Colonies generally robust; dendroid, encrusting, or massive. (Ordovician - Triassic)
- **Cystoporata:** Colonies robust or delicate. (Ordovician - Triassic)
- **Cryptostomata:** Colonies typically delicate; foliate or dendroid. (Ordovician - Permian)
- **Fenestrata:** Colonies typically delicate; reticulate (net-like) or pinnate. (Ordovician - Triassic)
- **Tubuliporata**, or **Cyclostomata** (Ordovician - Recent)

Bryozoa – Order Fenestrata

- ***Fenestella althaea* Hall**
- **Flat colonies of “lacy” bryozoa**
- Early Devonian, Albany Co., New York
- Silica replacement

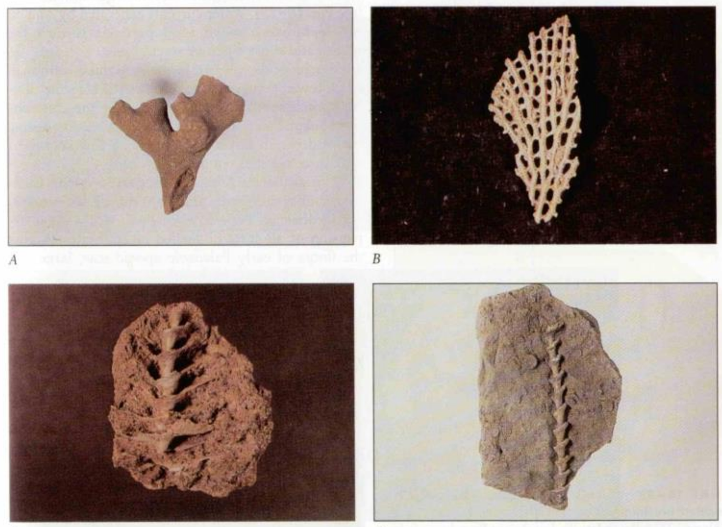
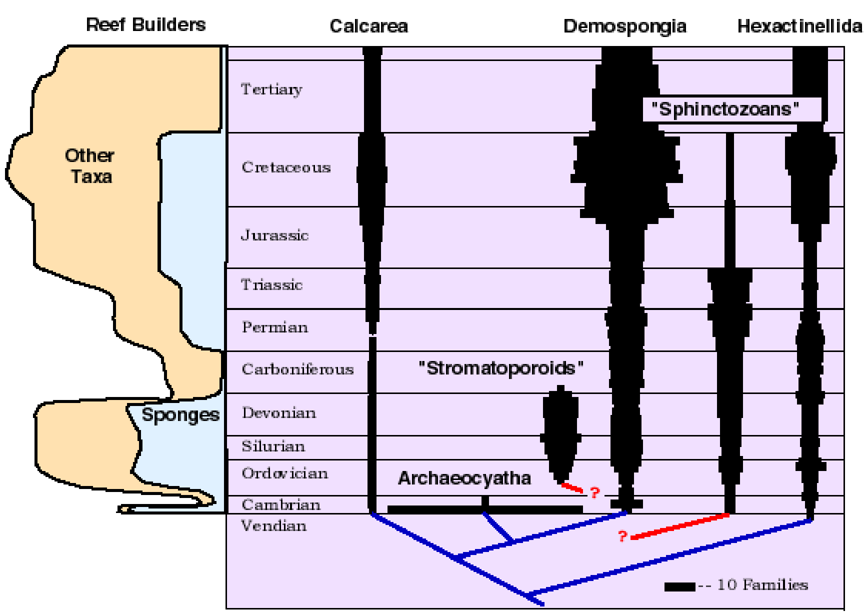
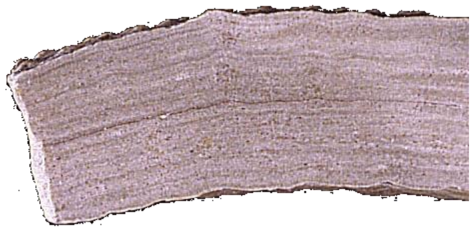


FIGURE 10-34 Paleozoic bryozoans. (A) The branching twig bryozoan *Hallopora* from the Ordovician of Kentucky. (B) *Fenestella*, a lacy bryozoan from Devonian limestones at the Falls of the Ohio River. (C) *Archimedes*, with part of the spirally encircling frond of lacy bryozoan colony attached and visible. (D) The central axis of *Archimedes*. Where were the zooecia located in this zoarium?

Porifera



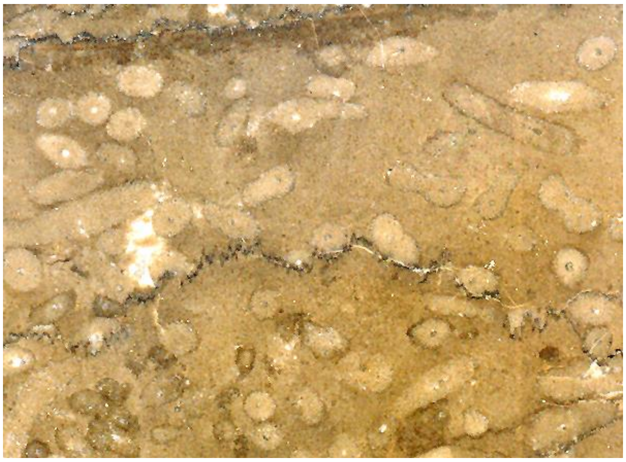
Stromatoporoids



Sponge-like, grew in sheet-like calcareous layers.

Dominant reef builders, Ordovician Period through the Devonian Period, a period of about 100 million years.

Stromatoporoids were marine colonial forms with a calcareous skeleton. They were important contributors to reef building during the Silurian and Devonian. Their relationship to other creatures is uncertain but they show some affinities with Porifera.
They consist of calcareous layers which, when weathered, show a charecteristic contour line pattern as seen in the specimen above.

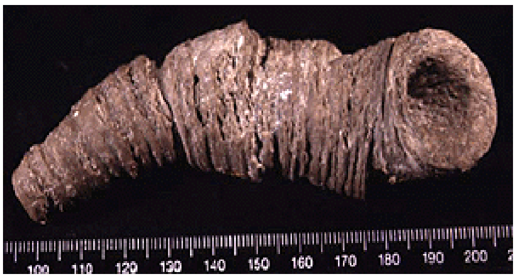


Amphipora floatstone in peloidal line mud matrix; note common stylolites"
Upper Devonian
Leduc Formation
Alberta

Cnidaria – Rugosa (solitary)

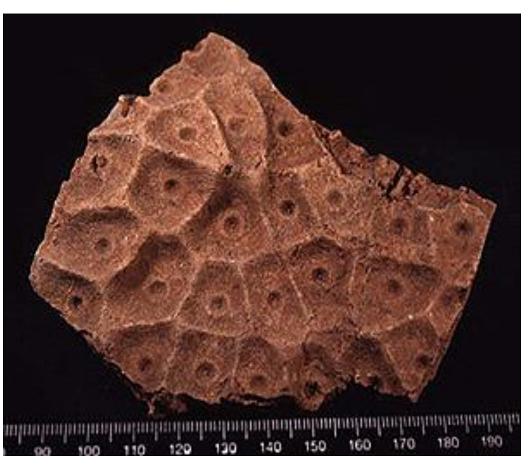
- Rugosa are an extinct group of corals that were abundant in Middle Ordovician to Late Permian
- Solitary rugosans are often referred to as "horn corals"
- Rugosa can also be colonial
- extinct at the end of the Permian, about 245 million years ago

Cnidaria – Rugosa (solitary)



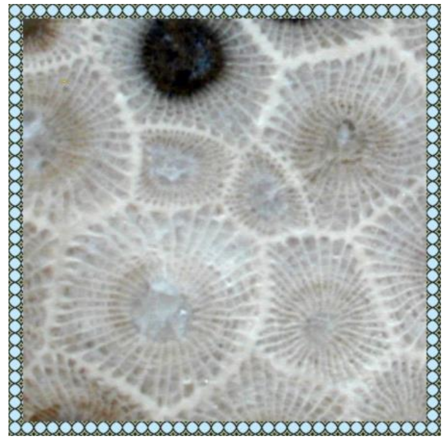
- ***Cystiphyllum conifollis***
- Solitary Rugose coral
- Middle Devonian, Ontario, Canada
- Recrystallization

Cnidaria – Rugosa (colonial)

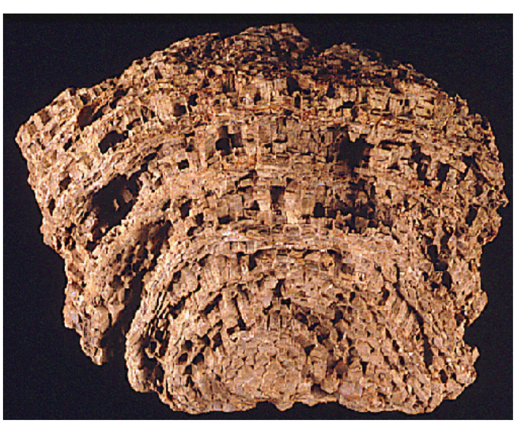


- ***Arachnophyllum pentagonum* Goldfuss**
- Colonial rugose coral
- Middle Silurian, Kentucky
- Silica replacement

Petoskey Stones – recrystallized colonial Devonian rugose corals

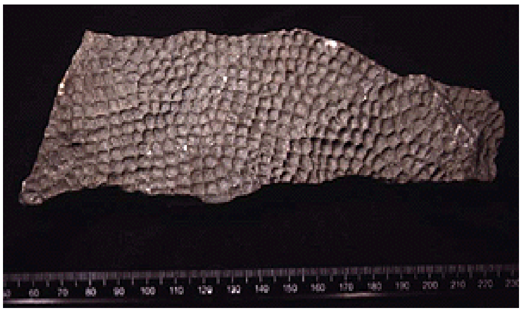



Tabulate corals



- Common from the Ordovician to the Permian
- Horizontal internal partitions known as **tabulae**
- Only occur as colonial forms, often forming substantial reefs
- extinct at the end of the Permian, about 245 million years ago

Tabulate corals



- ***Favosites favosus* (Goldfuss)**
- Honeycomb coral
- Middle Silurian, Anticosti Island, Quebec, Canada
- Recrystallization

Genus *Halysites*

Phylum Echinodermata

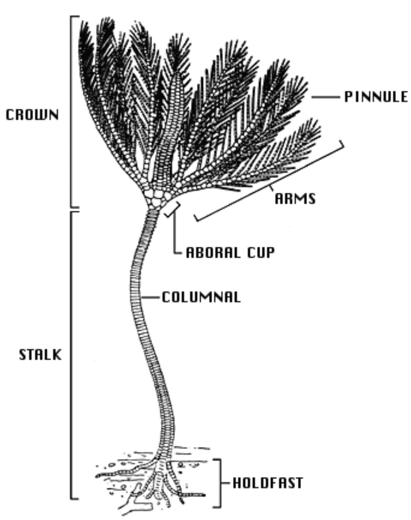
Subphylum Blastozoa (jablovci a poupěnci)
..........Class Eocrinoidea (Cambrian - Silurian, 30-32 genera)
..........Class Parablastoidea (Ordovician, 3 genera)
..........Class Rhombifera = Cystoidea in part (Ordovician - Devonian, 60 genera)
..........Class Diploporita = Cystoidea in part (Ordovician - Devonian, 42 genera)
..........Class Blastoidea (Silurian - Permian, 95 genera)

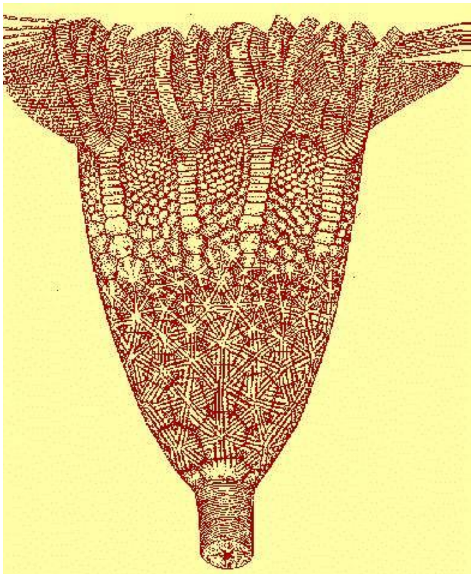
Subphylum Crinozoa (lilijice)
..........Class Crinoidea - sea lilies (Cambrian? Early Ordovician - Recent, 1005 genera)
..........Class Paracrinoidea (Ordovician - Silurian, 13-15 genera)

Subphylum Echinozoa (ježovky a sumýši)
..........**Class Echinoidea (Sea Urchins) (Ordovician - Recent, 765 genera)**
..........**Class Holothuroidea (Sea Cucumbers) (Ordovician - Recent, 200 genera)**
..........Class Edrioasteroidea (Early Cambrian - Carboniferous, 35 genera)
..........Class Edrioblastoidea (Ordovician, 1 genus)
..........Class Helicoplacoidea (Cambrian, 3 genera)
..........Class Cyclocystoidea (Ordovician - Devonian, 8 genera)

Subphylum Asterozoa (hvězdice a hadice)
..........Class Asteroidea - starfish - (Early Ordovician - Recent, 430 genera)
..........Class Ophiuroidea - Brittle Stars -(Ordovician - Recent, 325 genera)

Subphylum Homalozoa (karpoidi)
..........Class Stylophora (Cambrian - Devonian, 32 genera)
..........Class Homoiostelea (Cambrian - Devonian, 12-13 genera)
..........Class Homostelea (Cambrian, 3 genera)
..........Class Ctenocystoidea (Cambrian, 2 genera)





Scyphocrinites

Echinodermata - Crinoidea

- *Agriocrinus sp*,
- Devonian Hunsruck Slate of western Germany
- Partly compressed, recrystallized and partly pyrite replaced

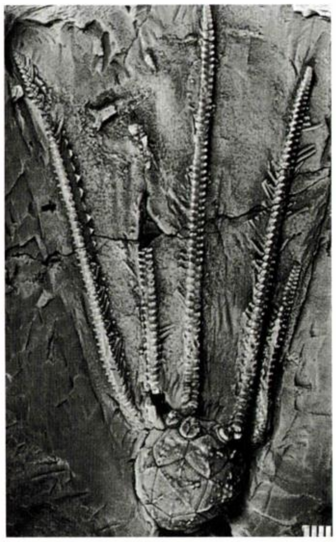
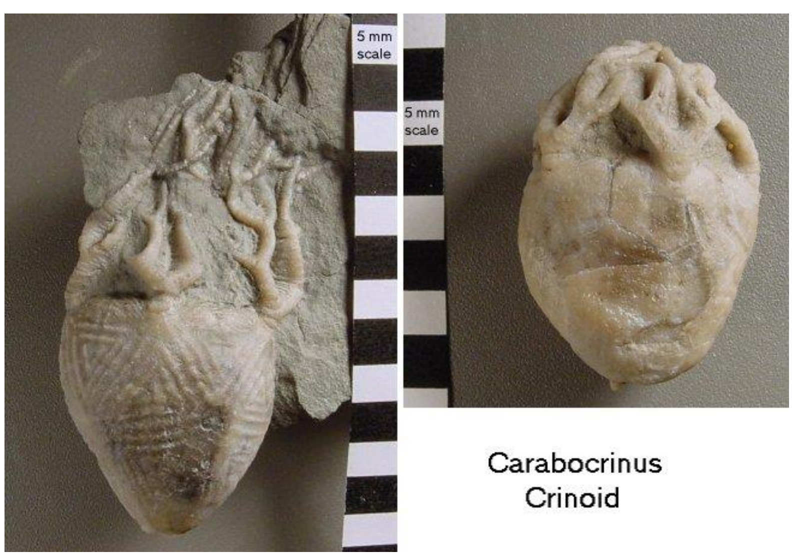


FIGURE 10–56 A well-preserved specimen of the Silurian cystoid *Caryocrinites ornatus* from the Lockport Shale of New York. *(From Sprinkle, J. 1975.* J. Paleo. *49(6):1062–1073.)*

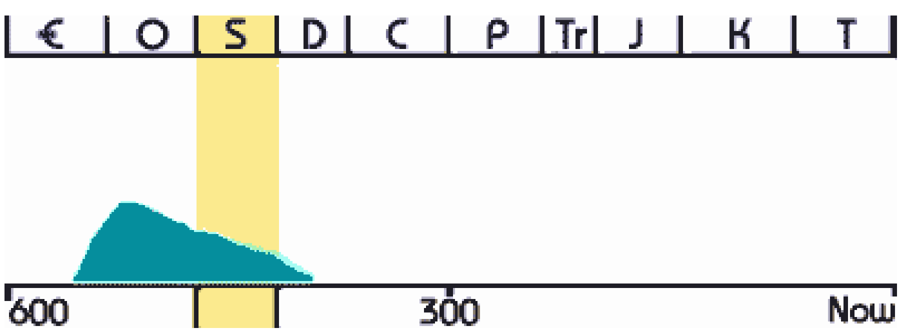


Carabocrinus
Crinoid

Echinodermata - Asterozoa

- ***Devonaster eucharie* (Hall**
- **Middle Devonian, Ulster Co., New York**
- **External Mold in shale**

Graptoloidi

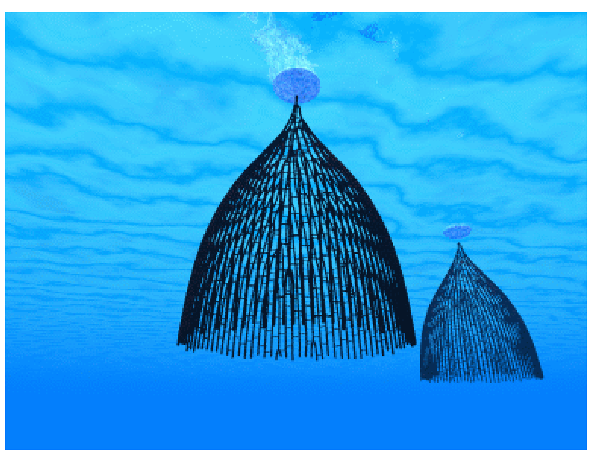


Kingdom Animalia, Phylum Protochordata

- Graptolithinia – **Graptolites –** planktic or benthic
  - Appear as “pencil-like” marks on shale
  - Are colonial
  - Animals live in theca along outside of colony

Climacograptus

Didymograptus from Victoria, Australia
(Lower Ordovician)
Graptolites range from the middle Cambrian to the Carboniferous. Dendroidea are found across this entire span while Graptoloida are found from the Ordovician until the early Silurian. Graptolites are most commonly found in deep water, dysoxic facies (black shales), but do extend into shallow facies. Because they did not biomineralize an easily preservable skeleton they are nearly always carbonized.



The dendroid graptolite *Rhabdinopora*, lower Ordovician. Did it float suspended from a "bubble", like a Portuguese Man-o-war, or as epiplankton, attached to seaweed? A colony like this could become at least a foot long.

Chordata

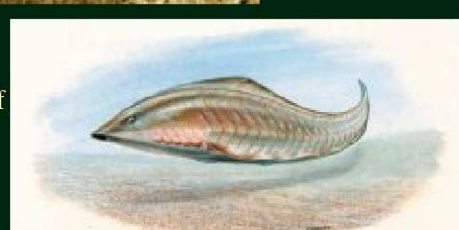
The fossil cephalochordate *Pikaia*. Cephalochordates are rare as fossils but are now known to extend back 530 million years. The leading hypothesis is that the common ancestor of all vertebrates was a lancelet-like organism — if not *Pikaia*, then something like it.

Haikouella and *Myllokunmingia*

- Described in November 1999 from south China; 530 million years old (Early Cambrian)
- Completely soft-bodied; rather lancelet-like appearance, but probably more active lifestyle
- Complex pouched gills instead of simple slits, and W-shaped myomeres
- These are either the oldest vertebrates, or they're very close. . .

Fossil of *Myllokunmingia*

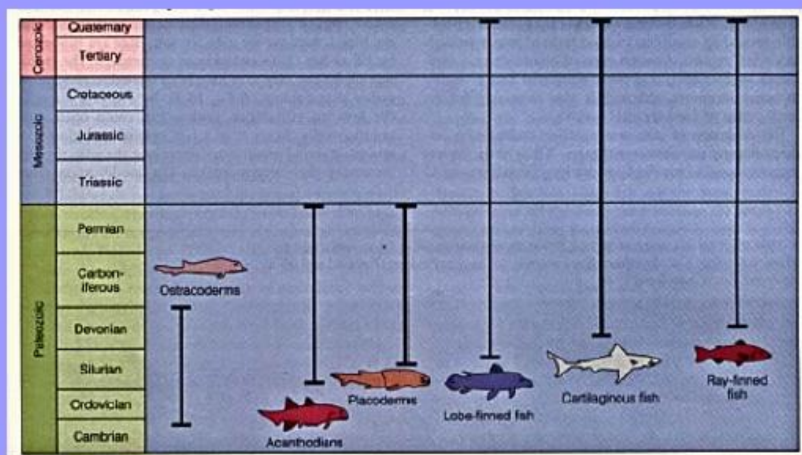
Reconstruction of living organism



Rybovití obratlovci

Fish

- Fish range from the Late Cambrian to the present and consist of five classes
  - ostracoderms, acanthodians, placoderms, cartilaginous fish, and the bony fish



KINGDOM: **ANIMALIA**
PHYLUM: **CHORDATA**

SUB-PHYLA: UROCHORDATA (sea squirts)
HEMICHORDATA (pterobranchia, graptoliti*) *CAMB.*
CEPHALOCHORDATA (mihule, sliznatky) *CAMB.*
CRANIATA (obratlovci) *CAMB.*

CLASSES: **CONODONTA*** *CAMB.*

AGNATHA (bezčelistné „ryby“) *CAMB.*
ACANTHODI (trnoplotví žraloci)* *SIL.*
PLACODERMI (pancířnaté ryby)* *SIL.*
CHONDRICHTHYES (paryby) *DEV*
OSTEICHTHYES (kostnaté ryby) *SIL.*

AMPHIBIA (obojživelníci) *DEV.*
REPTILIA (plazi) *CARB.*
AVES (ptáci) *JURASSIC*
MAMMALIA (savci) *TRIASSIC*

Agnatha

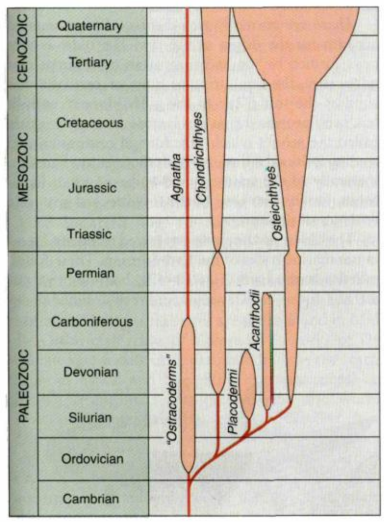


FIGURE 10–64 Evolution of the five major categories of fishes. The width of the vertical red areas indicates the approximate relative abundance of each group. *(From many authors.)*

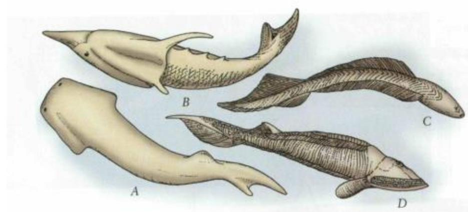
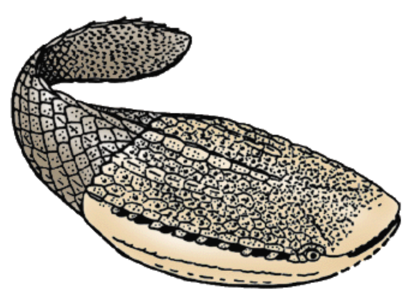
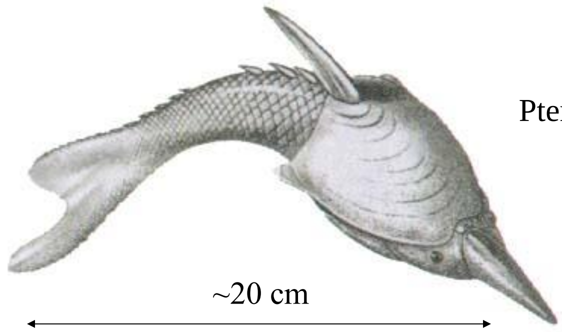


FIGURE 10–66 The early Paleozoic ostracoderms. (A) *Thelodus*, (B) *Pteraspis*, (C) *Jamoytius*, and (D) *Hemicyclaspis* drawn to the same scale.



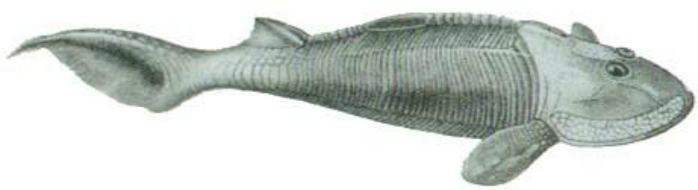
Astraspis

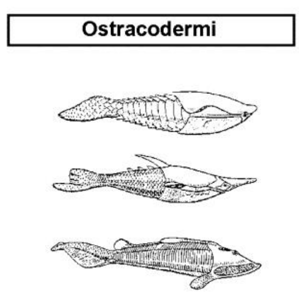
Devonian Jawless Fish

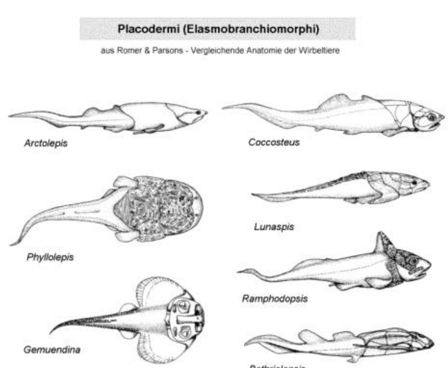


Pteraspis

Hemicyclaspis







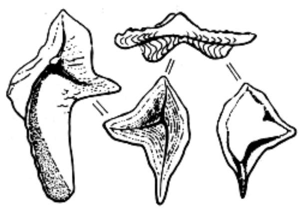
Conodont animals
(Conodontophorida)

- Conodont teeth are very common fossils, known since early 1800s, but animal body only described in 1983
- May or may not be true vertebrates
  - **Vertebrate characters** sense organs with capsules; $CaPO_4$ mineralization
  - **Non-vertebrate characters:** V-shaped myomeres; notochord but no trace of vertebrae
- 250+ million-year fossil history (Late Cambrian-Triassic)

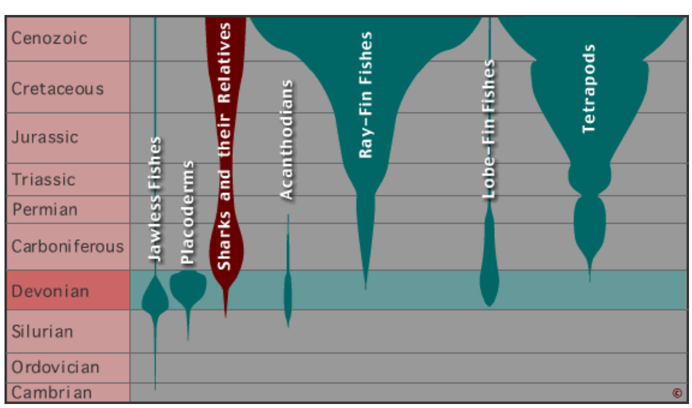
A single conodont. . .

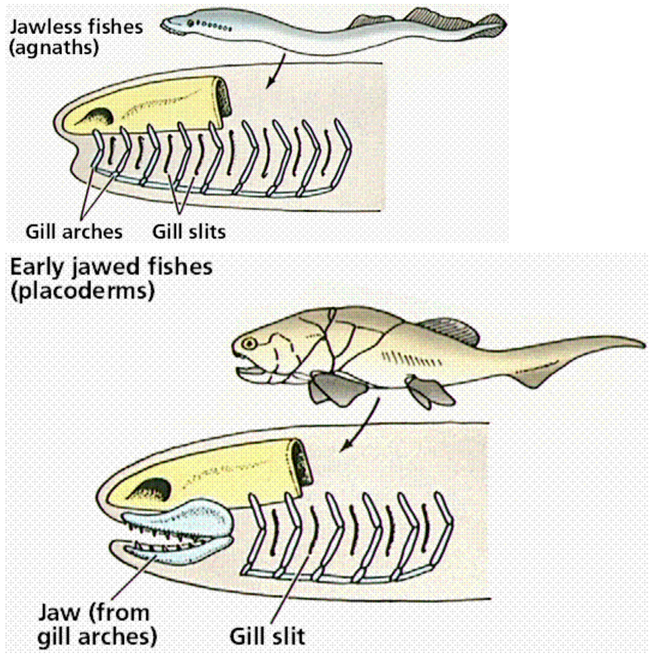
A conodont apparatus. . .

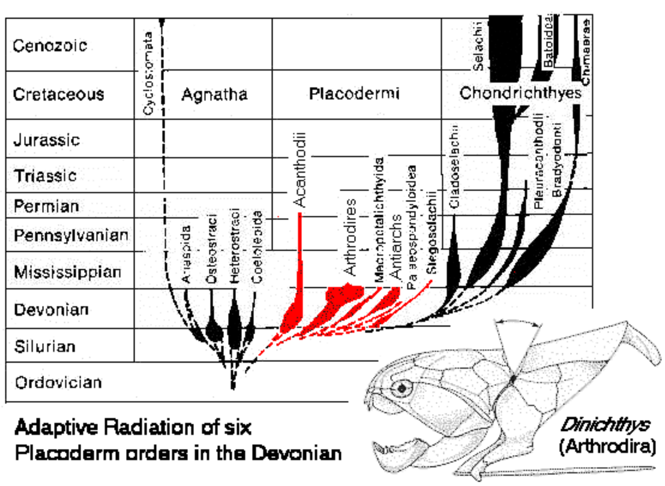
CONODONTA



Gnathostomata: čelistnatí







Adaptive Radiation of six
Placoderm orders in the Devonian

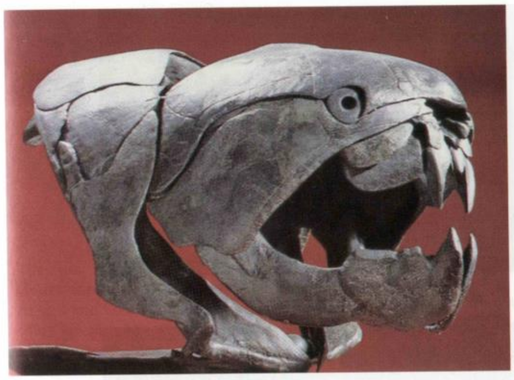
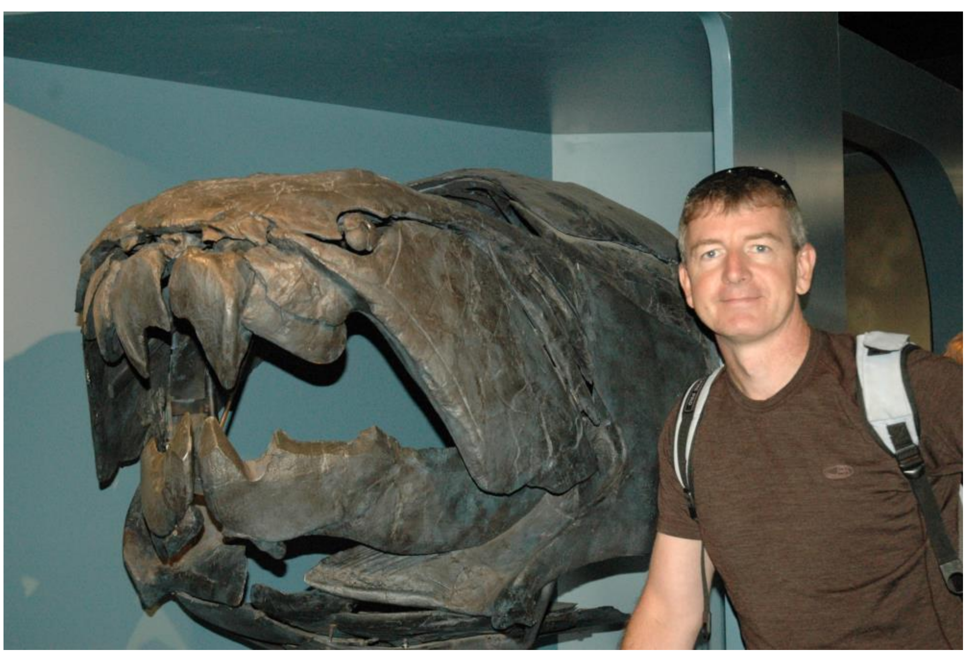
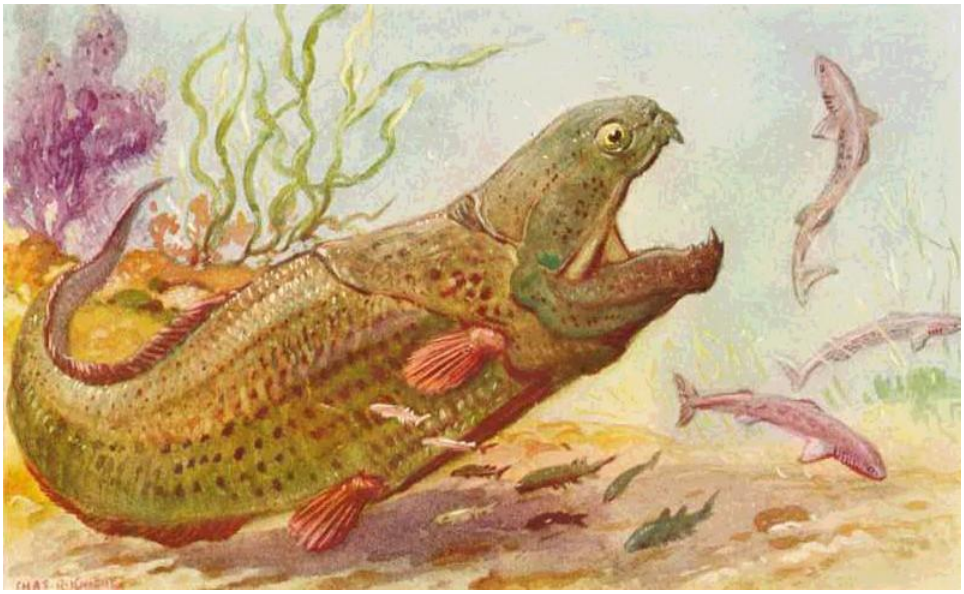
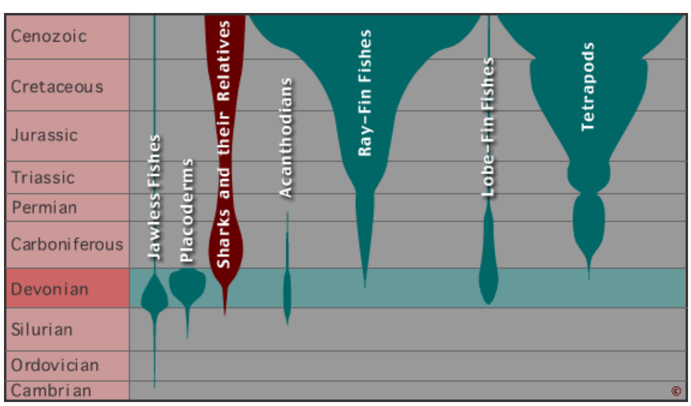


FIGURE 10–68 **The gigantic armored skull and thoracic shield of the formidable late Devonian placoderm fish known as *Dunkleosteus*.** *Dunkleosteus* was over 10 meters (about 30 feet) long. The skull shown here is about 1 meter tall. It is equipped with large bony cutting plates that functioned as teeth. Each eye socket was protected by a ring of four plates, and a special joint at the rear of the skull permitted the head to be raised and thereby provided for an extra large bite. *Dunkleosteus* ruled the seas 350 million years ago. *(Courtesy of the U. S. National Museum of Natural History, Smithsonian Institution; photograph by Chip Clark.)*





ACANTHODI


Cenozoic
Cretaceous
Jurassic
Triassic
Permian
Carboniferous
Devonian
Silurian
Ordovician
Cambrian
Jawless Fishes
Placoderms
Sharks and their Relatives
Acanthodians
Ray-Fin Fishes
Lobe-Fin Fishes
Tetrapods

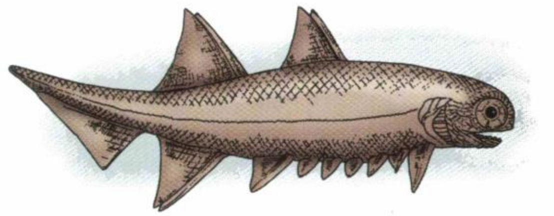
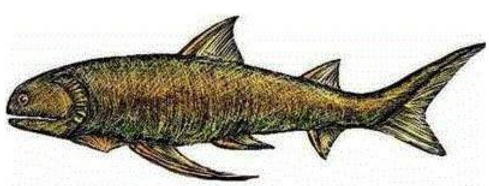
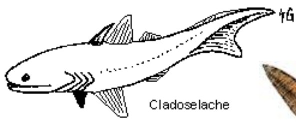


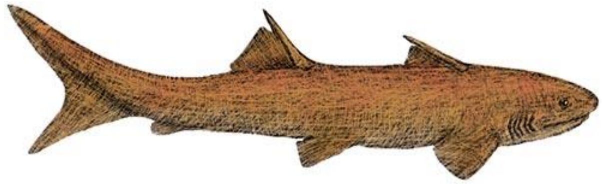
FIGURE 10–67 The Early Devonian acanthodian fish *Climatius*. *(After Romer, A. S. 1945.* Vertebrate Paleontology. *Chicago: University of Chicago Press.)*



Acanthodii

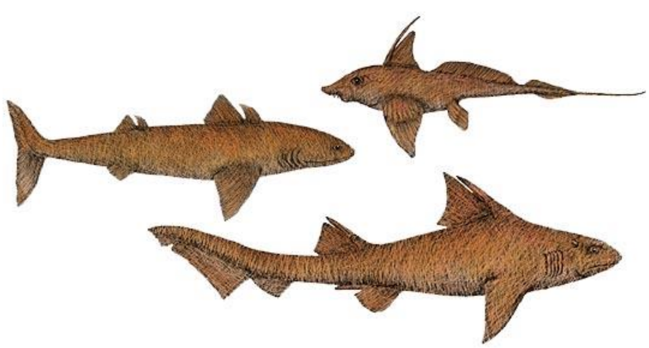


First sharks



Ctenacanthus sp, a Late Devonian and Carboniferous shark

The very earliest signs of sharks are minute fossil scales and teeth which are found in rocks from the late Silurian to early Devonian period {around 400 million years ago). It becomes more and more difficult, however, to identify shark scales in older rocks because they closely resemble those from jawless fishes called the lodonts, which lived at the same time. Only microscopic differences separate shark and the lodont scales, and the two kinds seem to become more and more alike the further one goes back.



Cladoselache (top left, Middle Devonian), *Ischyodus* (top right, Upper Jurassic) and *Hybodus* (bottom, Lower Jurassic) ©

Kostnaté ryby (Osteichtyes)

There are two groups of bony fish

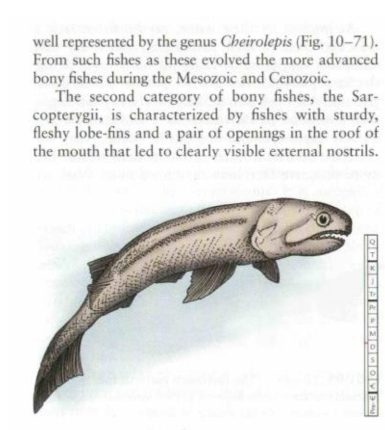
1.Paprskoploutvé ryby
began their evolution in Devonian lakes and streams (freshwater) and then spread to the sea. They are the **dominant fishes of the modern world**.

2.Sarcopterygii
Lobe-finned fish have muscular fins with articulating bones. There are two groups of lobe finned fish.

a.Dvojdyšné ryby (Dipnoi)
Lungfish live today in freshwater.

a.Lalokoploutvé ryby (Crossopterygii)
This is an important group of lobe-finned fish because it **gave rise to the amphibians** during the Devonian.

Paprskoploutvé ryby


well represented by the genus *Cheirolepis* (Fig. 10–71). From such fishes as these evolved the more advanced bony fishes during the Mesozoic and Cenozoic.
The second category of bony fishes, the Sarcopterygii, is characterized by fishes with sturdy, fleshy lobe-fins and a pair of openings in the roof of the mouth that led to clearly visible external nostrils.

Dvojdyšní

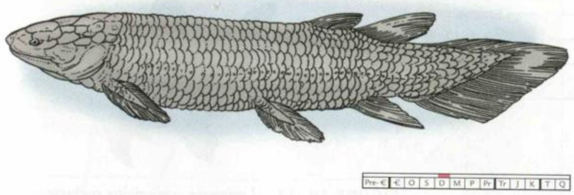
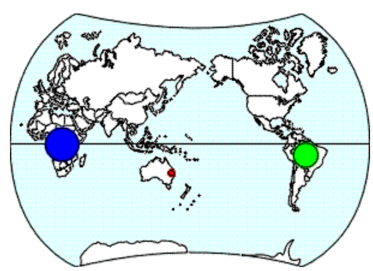


FIGURE 10–72 *Dipterus*, a Devonian lungfish.

Dvojdyšní v moderním světě



Protopterus ssp

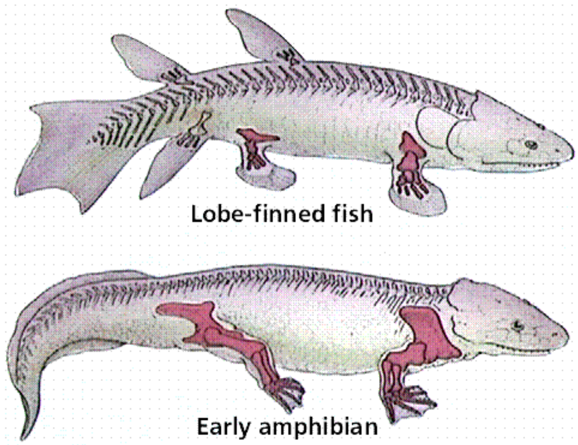
Lepidosiren paradoxa

Lalokoploutvé ryby

Eusthenopteron

Lalokoploutvé ryby v moderním světě: *Latimeria*

Vývoj končetin: lalokoploutví → tetrapodi



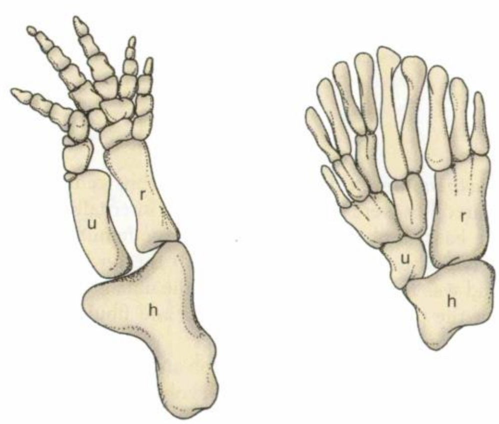


FIGURE 10–73 Comparison of the limb bones of a crossopterygian fish (upper right) and an early amphibian. (Some early amphibians may have had more than five digits.) *(From Levin, H. L. 1975.* Life Through Time. *Dubuque, IA: William C. Brown Co.)*

První čtvernožci: *Ichthyostega* (obojživelníci)

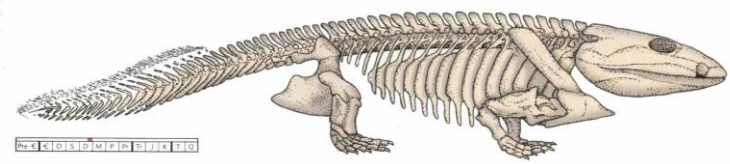
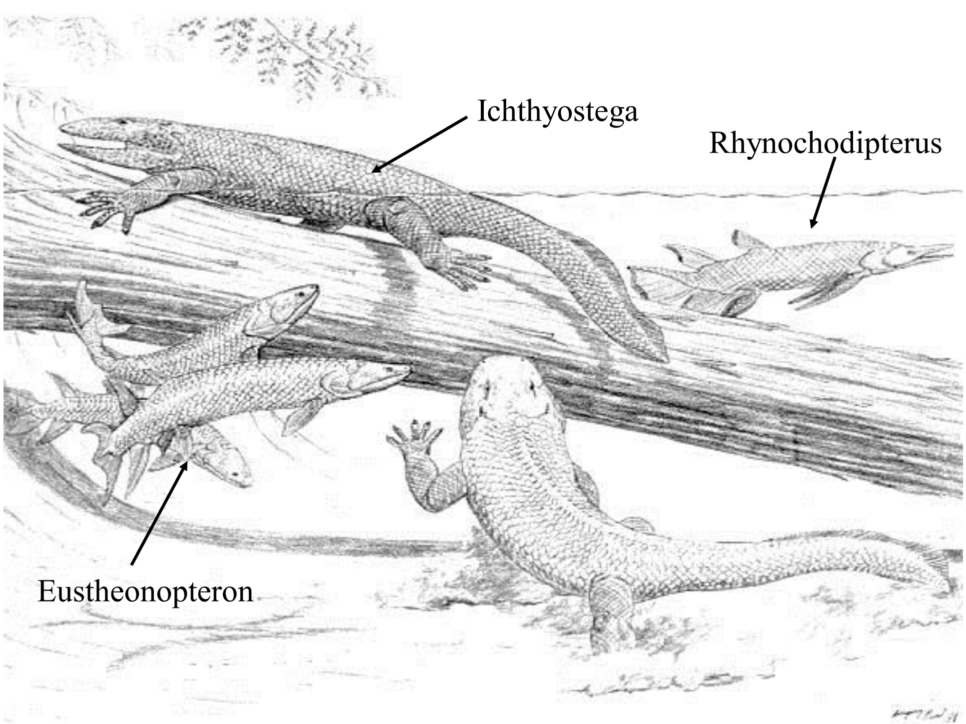


FIGURE 10–79 The skeleton of *Ichthyostega* still retains the fishlike form of its crossopterygian ancestors. *(From Levin, H. L. 1975. Life Through Time. Dubuque, IA: William C. Brown Co.)*



What is a mass extinction?

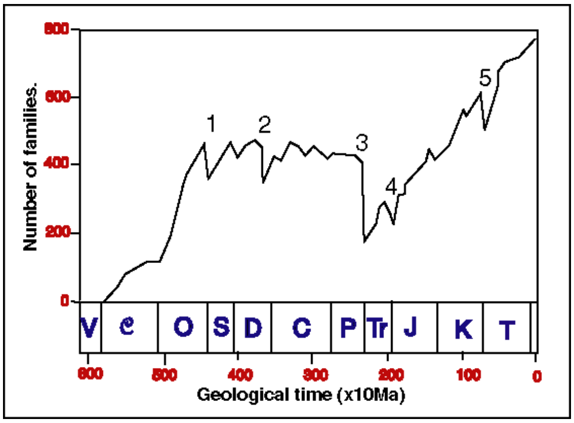
- A **mass extinction** occurs when a large fraction of all living species becomes rapidly extinct.
- The fossil record shows that at least five major mass extinctions have occurred in the past 500 million years.
- Impacts of asteroids on Earth are suspected as a primary cause of mass extinction.

The Paleozoic Era

Mass Extinctions and

Evolutionary Changes

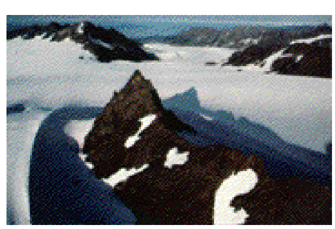
- Three of the five major mass extinctions occurred during the Paleozoic era:
  - At the end of the **Ordovician** period,
  - during the late **Devonian** period, and
  - at the end of the **Permian** period.

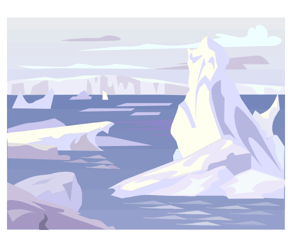


- **The graph shows when the five extinctions occurred. As you can see, the Permian extinction was the most severe.**

The Ordovician Extinction

- This extinction occurred at end of the period, about 440-450 mya.
- It is thought to be caused by a global cooling, which caused the continent Gondwana to glaciate. Geologists have found glacial deposits in the Saharan desert, which provided the evidence for this theory.

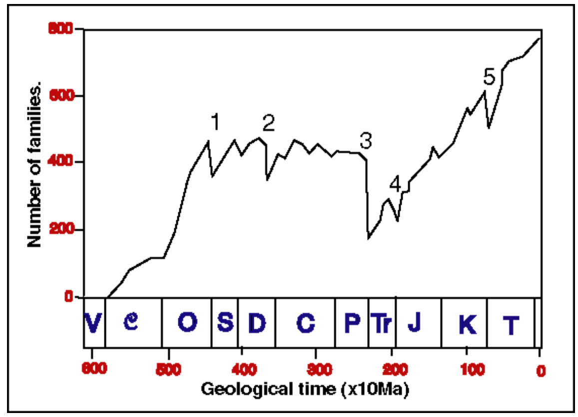




- Since more water was in ice form, the sea level lowered all over the world, causing a reduction of space for life on continental shelves.
- The most affected animal group was the *marine invertebrates*, in which more than 100 families were wiped out.

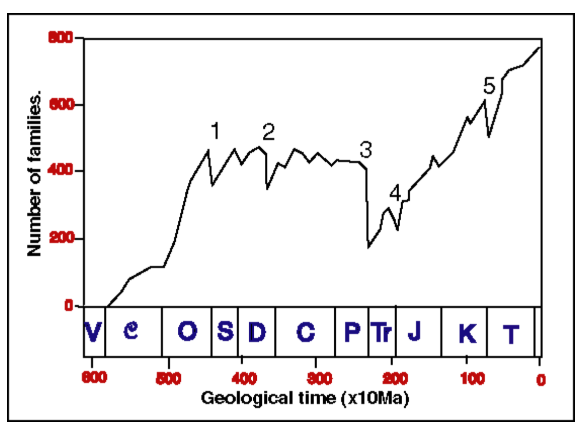
Frasnian/Famennian extinction: one of the “Big Five“

- Only ~15 % of Frasnian brachiopod genera survive in Famennian
- A similar decline in ammonoids trilobites, conodonts, gastropods and trilobites
- Disapperanace of coral-stromatoporoif reef communities
- Severe extinction of acritarchs (the only abundant phytoplankton group in Devonian)
- Nearly complete disapperance of placoderms
- little effect on land animals, mostly affecting (again) the marine life



Frasnian/Famennian extinction: one of the “Big Five“

- climate cooling
- glass sponges, which today are restricted to cool waters, began to thrive where formerly successful tropical marine fauna had become extinct.
- glacial deposits have been found in northern Brazil
- Sea-level fluctuation
- meteorite impacts have also been thought a possible cause of this mass extinction, although the evidence remains inconclusive.



Devonian bioevents: not only the F/F

- Lochkovian/Pragian E
- Basal Zlíchov E
- Daleje E
- Basal Choteč E
- Kačák E
- Taghanic E
- Frasnes E
- Middlesex E
- L + U Kellwasser E
- Nehden E
- Annulata E
- Dasberg E
- Hangenberg E

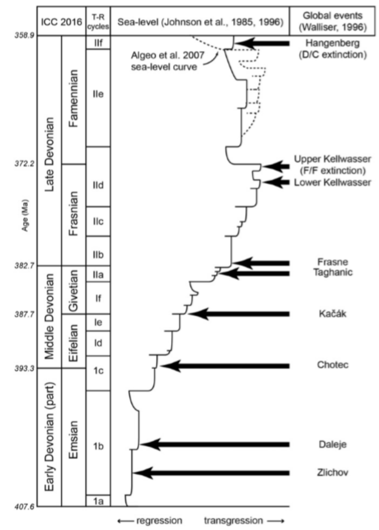
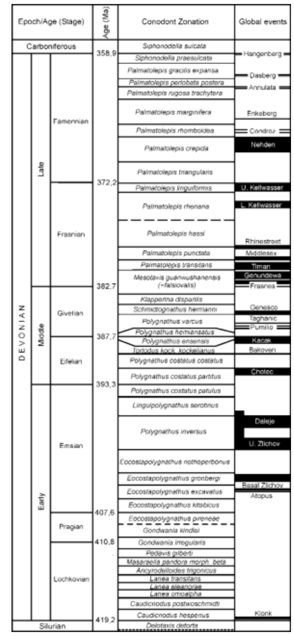


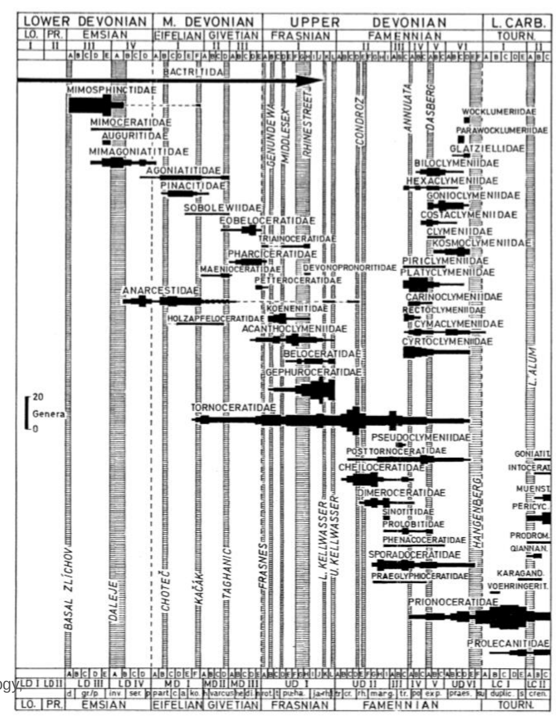
Fig. 3. Devonian chronostratigraphy, eustatic sea-level history (modified from Johnson et al., 1985, 1996, with alternative interpretation [dashed line] for the Late Devonian part based on Algeo et al., 2007) and global events (after Walliser, 1996). Repeated widespread black shales record transgressive anoxic events, each of which are associated with minor extinctions.



Bond DPG, Grasby SE (2017) Palaeogeography, Palaeoclimatology, Palaeoecology 478: 3-29.

Devonian bioevents

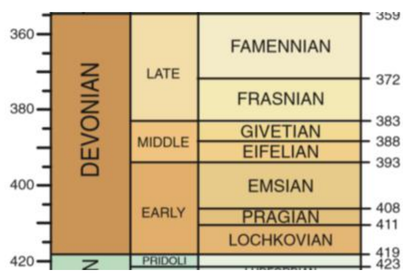
Generic diversity of ammonoids through time and major bioevents of the Devonian



House MR (2002) Palaeogeography, Palaeoclimatology, Palaeoecology 181: 5-25.

Devonian bioevents

Extinction of invertebrate marine families for each stage of the Devonian (after Benton, 1993, modified)



TAXON	SIL.		DEVONIAN							VIS.
		PRD	LOK	PRA	EMS	EIF	GIV	FRA	FAM	TOU
PROTOZOA		2	0	0	0	0	0	2	2	
PORIFERA		0	0	1	0	1	0	3	1	
STROMATOPOROIDS		1	1	0	0	0	0	6	6	
TABULATA etc		3	2	1	2	7	2	3	0	
RUGOSA etc.		0	4	1	3	6	18	3	5	
GASTROPODA etc		0	0	1	3	1	6	1	1	
NAUTILOIDEA		5	4	0	1	5	5	2	12	
AMMONOIDEA		0	0	0	4	0	6	9	24	
COLEOIDEA		0	0	0	3	0	0	0	0	
BIVALVIA		1	0	0	2	2	3	1	0	
TENTACULITIDA etc		0	3	0	0	1	1	4	3	
ANNELIDA		2	0	0	0	0	0	3	0	
TRILOBITES, EURYPTS etc		5	1	5	5	2	5	8	3	
CRUSTACEA pars		1	0	0	0	1	0	0	3	
OSTRACODA		1	1	0	0	2	0	2	4	
BRACHIOPODA		6	6	6	7	12	14	15	2	
BRYOZOA		1	0	0	1	0	4	1	2	
ECHINODERMATA		0	3	2	7	3	5	4	2	
GRAPTOLITHINA		1	1	0	1	0	0	0	0	
MISCELLANEA		0	0	0	0	1	1	0	0	
CONODONTA		1	1	1	0	0	1	0	3	
EXTINCT IN STAGE		30	27	18	39	44	71	67	73	
TOTAL FAMILIES IN STAGE		466	468	479	504	498	493	449	449	444
EXTINCT/TOTAL X 100		6.4	5.8	3.8	7.7	8.8	14.4	14.9	16.3	

House MR (2002) Palaeogeography, Palaeoclimatology, Palaeoecology 181: 5-25.

Devonian biodiversity-loss events (bioevents)

Major Devonian biodiversity losses:

- I-D: intra-Devonian events
- F/F event
- D/C event

Major bolide impacts:

- Siljan Ring (Sweden)

Large igneous provinces:

- Viluy (Siberia)
- PDD (Pripyat-Dnieper-Donetsk)

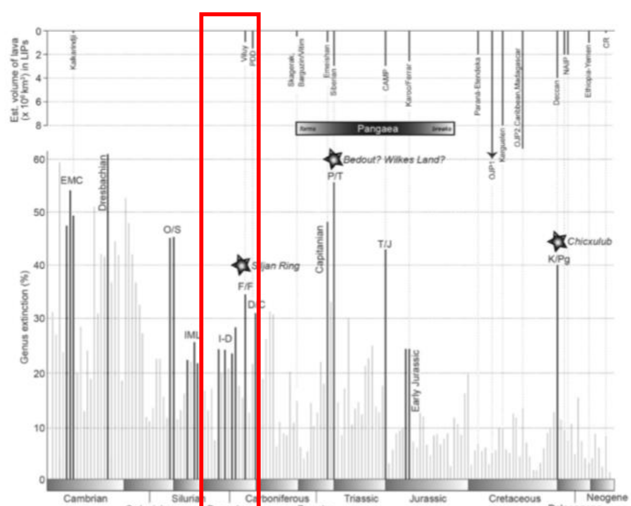


Fig. 8. Genus extinction magnitude through the Phanerozoic (based on Sepkoski, 1996, 2002; and Bambach et al., 2004) versus the age and estimated original volume of large igneous provinces (volume estimates based on Encarnación et al., 1996; Courtillot et al., 1999; Marzoli et al., 1999; Olsen, 1999; Fedorenko et al., 2000; Courtillot and Renne, 2003; Glass and Phillips, 2006; Courtillot et al., 2010; Kuzmin et al., 2010; Kravchinsky, 2012) and the age of supposed bolide impact structures (grey/black stars). Extinction events: EMC = Early to Middle Cambrian, comprising a series of (related?) events around the Cambrian Series 2/3 boundary; O/S = Ordovician/Silurian; IME = Ireviken, Mulde and Lau Events; I-D = a series of intra-Devonian events; F/F = Frasnian/Famennian (Kellwasser Event); D/C = Devonian/Carboniferous (Hangenberg Event); P/T = Permian/Triassic; T/J = Triassic/Jurassic; and K/Pg = Cretaceous/Paleogene. Large igneous provinces: PDD = Pripyat-Dnieper-Donets rift; CAMP = Central Atlantic Magmatic Province; OJP 1/OJP 2 = Ontong Java Plateau phases 1 and 2; NAIP = North Atlantic Igneous Province; CR = Columbia River Basalt Group. Note the apparent correlation between mass extinction events (peaks in genus extinction) and LIP emplacement, particularly during the time of Pangaean continental configuration. Adapted from Bond et al. (2010a) and Bond and Wignall (2014).

Bond DPG, Grasby SE (2017) Palaeogeography, Palaeoclimatology, Palaeoecology 478: 3-29.

Isotope record at the D/C boundary GSSP, La Serre Hangenberg E.

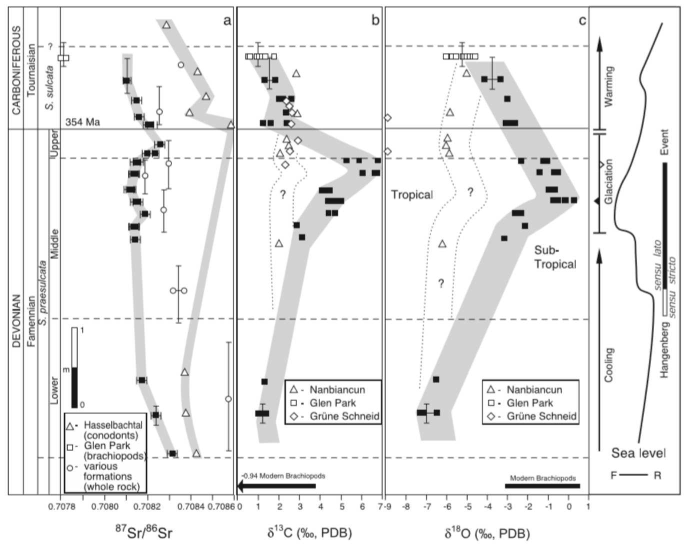
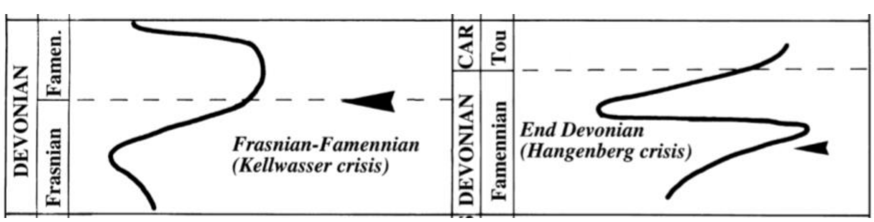


Fig. 9. Strontium, carbon and oxygen isotope biochemostratigraphic summary diagrams. (a) shows the Sr isotope trend established for the DevonianCarboniferous boundary interval with other data superimposed from the Glen Park Formation (brachiopods-Illinois, Mii et al., 1999), various formations and localities (whole rock, Denison et al., 1994, 1997, in ascending order: Pilot, Holt Summit, Palliser, Louisiana, Pilton and New Albany; Yang et al., 1988, Nanbiancun, China), and from Hasselbachtal (conodonts, Ku ¨rschner et al., 1993). The age of the DC boundary is based on information from Claoue ´-Long et al. (1992). (b) depicts the C isotope trend for the DevonianCarboniferous boundary interval with other brachiopod isotope data from the Glen Park Formation (Mii et al., 1999), Nanbiancun Formation (Huang et al., 1988), and matrix (whole rock) data from the Gru ¨ne Schneid section (Scho ¨nlaub et al., 1992). Tropical trend inferred from brachiopod isotope data from Nanbiancun of southern China. (c) shows the O isotope trend and data for the Devonian–Carboniferous boundary supplemented by isotope data from the Glen Park, Nanbiancun and Gru ¨ne Schneid sections. Tropical and subtropical climatic trends based on brachiopod data of this and Nanbiancun studies (Huang et al., 1988). Duration of the Hangenberg Event (sensu stricto Walliser, 1984 open and solid part of bar, sensu lato solid part of bar only), general climatic information from Streel et al. (2000), and paleoceanographic information (sea level, F—fall, R—rise) from Feist et al. (2000). Solid triangle on 'glaciation' bar indicates glacial maximum, whereas the open triangle indicates the CO2 atm drawdown/organic matter burial maximum.

Brand et al. (2004) Palaegeography, Palaeoclimatology, Palaeoecology 205: 337_357.

Devonian bioevents and sea-level changes: summary



Hallam A, Wignall PB (1999) Earth-Science Reviews 48: 217-250.

This extinction, cited as the second most devastating extinction to marine communities in earth history,

disappearance of **one third of all brachiopod** and **bryozoan** families

numerous groups of **conodonts**, **trilobites**, and **graptolites**.

In total, more than **one hundred families** of marine invertebrates perished in this extinction.

https://www.youtube.com/watch?v=q05JFgXnZDc